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Observations on Intertidal Organism Associations of St. Catherines Island, Georgia. II. Morphology and Distribution of *Littorina irrorata* (Say)

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ABSTRACT

The marsh periwinkle *Littorina irrorata* (Say) occurs in a variety of *Spartina* marsh settings on St. Catherines Island, Georgia. Cohorts of *L. irrorata* were collected at four marsh localities and control grids were monitored over a three-week period. In addition, a fossil population was collected from a relict marsh mud. Each sample was subjected to detailed morphometric analysis using univariate, bivariate, and multivariate techniques.

Adult size of *L. irrorata* is inversely related to population density and density, in turn, is directly proportional to the abundance of *Spartina* grass. Progenesis appears to be the adaptive strategy adopted for size decrease. Aperture shape exhibited the least variation and was relatively independent of translation rate, whorl expansion rate,

aperture angle, and total width. Larger apertural area was correlated with low marsh environments ("wetter" conditions). Total width of *L. irrorata* proved to be a better indicator of population structure than total height and should be used in the construction of survivorship curves for this species. The fossil population sample apparently reflects substantially different growth dynamics, achieving adult size at fewer than six whorls.

L. irrorata is a potentially useful tool for paleoenvironmental reconstructions. The species appears to exhibit limited lateral motility and has a strong distributional dependence upon *Spartina* grass. Monitoring cohorts of *L. irrorata* demonstrated a direct relationship between population density and short-term stability of population size.

INTRODUCTION

The marsh periwinkle *Littorina irrorata* (Say) is a conspicuous and abundant inhabitant

of the South Atlantic and Gulf coasts, especially during the summer months when

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it climbs high upon the stems of the marsh grass *Spartina alterniflora*. To date, study of *L. irrorata* has focused on its life history, behavior, and, to some extent, population structure (Smalley, 1958; Shirley et al., 1978; Stiven and Hunter, 1976; Hamilton, 1976, 1977, 1978; Shirley and Findley, 1978; Bingham, 1972a, 1972b; Hall, 1973). Very little attention has been directed toward aspects of shell morphology and ecophenotypic variation (Bingham, 1972c; Phillips and Newcombe, 1937).

The primary objective of our study was to determine the effects of environmental variation on the shell morphology of *L. irrorata* on St. Catherines Island, Georgia. We considered a variety of physical parameters, such as marsh type, intertidal exposure, and wave energy, as well as aspects of population density and motility. In addition, a "fossil" population sample from a relict marsh was included in order to evaluate the potential utility of *Littorina irrorata* in paleoenvironmental reconstruction.

LIFE HISTORY AND BEHAVIOR

Littorina irrorata has an extensive geographic range along the eastern coast of the United States, and is often abundant in intertidal and supratidal *Spartina* marshes from New York to Texas (Shirley and Findley, 1978). Unlike *Littorina littorea* (L.), an introduced species of the central and north-eastern Atlantic coasts, *L. irrorata* exhibits a strong substrate preference. *L. irrorata* only inhabits areas of living *Spartina*, or, less commonly, *Juncus* vegetation where it can be found in clumps at the base of the marsh grass stems during low tide on hot, sunny days and crawling up and down the stems just above the advancing and receding tides (fig. 1). *L. irrorata* is most active during low tides at night or on cloudy days (Hamilton, 1977; Shirley and Findley, 1978). As noted by Smalley (1958), *L. irrorata* is seldom found on the margins of tidal creeks and is most abundant among the short *Spartina* grass of the high-marsh area. The preferred habitat of *L. irrorata* effectively prevents direct contact with most other gastropods, although the coffee bean snail *Melampus bidentatus* Say occasionally shows minimal distributional overlap with *L. irrorata* at the extreme su-

pratidal range of the latter. This situation is in marked contrast to that of *Littorina littorea* (L.), where the common mud snail *Ilyanassa obsoleta* Say is being competitively displaced in many of its habitats due to a reciprocal niche overlap of the two species (Brenchley and Carlton, 1983; Bertness, 1984).

The food preferences of *L. irrorata* also illustrate the strong dependence of that species on *Spartina* grass. In a study of *L. irrorata* populations in Louisiana salt marshes, Alexander (1976) determined that the marsh periwinkle's primary energy source was plant detritus and associated epiphytes (Stiven and Kuenzler, 1979). Stiven and Kuenzler (1979) have challenged the conventional concept that *Spartina* debris constitutes an overabundant (i.e., nonlimiting) resource and support a consideration of the effects of food and space on the distribution, density, and growth of *L. irrorata*.

Both the short- and long-term migration of *L. irrorata* has been studied (Hamilton, 1976, 1977, 1978). Daily movement involves low-tide foraging over the substrate near the bases of *Spartina* stems and vertical movement up the stems, presumably in avoidance of predators, mainly the blue crab *Callinectes sapidus* Rathbun. The vertical migration is aided by visual identification of plant stems and by trail following (Hall, 1973; Hamilton, 1977). Low-tide movement is very limited. Hamilton (1977) marked adult snails in a marsh of the Florida Gulf and recorded average resultant distances traveled of 11.2 cm (SD = 19.5 cm) during a low-tide period. Long-term movements of *L. irrorata* include an offshore migration during fall and winter (only 1 m displacement for a Florida Gulf population of *L. irrorata*), which is possibly more extensive in northern populations (Hamilton, 1978). Smalley (1958) also observed that *L. irrorata* populations on Sapelo Island, Georgia exhibited a seasonal migrational pattern, descending to the floor of the marshes during the cold winter months where they remained clumped around the bases of *Spartina* stems. In addition, he noted that *L. irrorata* was more active during spring tides when the high marsh was flooded twice daily and less active during neap tides when the high marsh was relatively drier.



Fig. 1. *Littorina irrorata* at the base of short marsh grass (*Spartina alterniflora*), English Cut Marsh (station 10).

Reproductive strategies of *L. irrorata* have been elaborated by Smalley (1958) and Bingham (1972c). Eggs are individually deposited into the water and hatch into free-swimming larvae. Smalley (1958) found the larvae in tidal creeks from July to September and determined that young snails populated the *Spartina* marshes from July to October. The young snails possess 3.5 to 4 nuclear whorls at this time and reside in curled *Spartina* leaves or sandwiched between the leaves and stems. Young snails grow to shell heights of 4–5 mm before they are found crawling on outside surfaces.

Predictably, young *L. irrorata* individuals grow more rapidly and age/size classes become difficult to discern in larger (older) specimens (Smalley, 1958; Bingham, 1972c). An inverse relationship between rate of growth and population density of *L. irrorata* has been repeatedly observed: in Georgia marshes by Smalley (1958) and North Carolina marshes by Stiven and Kuenzler (1979) and Stiven and Hunter (1976). Maximum longevity of *L. irrorata* has been assessed at 13 years by Stiven and Hunter (1976). "Adult" individuals of *L. irrorata* have been somewhat arbitrarily defined for a Georgia high marsh as having a shell height of 13.5 mm (Smalley, 1958) and for a Florida Gulf marsh a height of 13.0 mm (Hamilton, 1977). Smalley (1958) noted a strongly bimodal size distribution of *L. irrorata* in a high-marsh setting. Bimodality was clearly attributable to young and "adult" individuals. Bingham (1972c) concluded that a bimodality he observed in "adult" specimens of *L. irrorata* from a Florida marsh was due to sexual dimorphism.

Microhabitat variation in density and size of *L. irrorata* has received some attention. Smalley (1958) noticed a marked difference in size distribution of the species between high marsh (short *Spartina*, firm substrate, and poor tidal flushing) and middle marsh (tall *Spartina*, lower elevation, soft substrate, and pronounced tidal water exchange). The high marsh harbored both small and large *L. irrorata* individuals whereas the middle marsh contained few large snails. Smalley assumed approximately equal recruitment potential for the two habitats and suggested that the middle marsh was more hostile to *L. irrorata*, as predators would more easily pen-

etrate the middle marsh at high tide. The density manipulations of *L. irrorata* in North Carolina marshes (Stiven and Kuenzler, 1979) suggest alternative explanations involving competition for space or feeding sites.

ST. CATHERINES ISLAND, GEORGIA

St. Catherines Island is one of the many barrier islands extending from Charleston, South Carolina to northern Florida. The island is approximately 40 miles south of Savannah, Georgia and is separated from the mainland of Georgia by about 5 miles of salt marshes, transected by the serpentine intra-coastal waterway (fig. 2). St. Catherines Island is a beach-ridge type island (Zeigler, 1959), about 10 miles long by 2 miles wide, displays pronounced lineation of ridges and swales, and is constructed primarily of well-sorted quartz sand.

About one-third of St. Catherines Island consists of a Pleistocene "core" of dune sand stabilized following the Silver Bluff submergence, approximately 37,000 to 25,000 years ago (Hoyt et al., 1964), when sea level dropped more than 100 m and the coast of Georgia extended up to 80 miles further east (Thomas et al., 1978). Subsequent sea-level rise severed the dunal "core" from the mainland, creating an island separated from the coast by first a lagoon and then, with increased sedimentation, a tidal marsh complex. The bulk of St. Catherines Island formed during the Holocene by development of beach ridges and tidal marshes on the seaward side of the island (Thomas et al., 1978; DePratter and Howard, 1977, 1980).

St. Catherines Island affords a wide variety of environmental settings, including heavily wooded areas (predominantly the northwestern portion) expansive salt marshes, tidal flats, and narrow sand beaches (Morris and Rollins, 1977). About 80 percent of the western shoreline and much of the east-central portion of the island consist of *Spartina* marshes. A ribbonlike barrier beach extends along the entire eastern margin of the island, punctuated by two tidal inlets: McQueen's and Seaside (fig. 3).

INTERTIDAL ENVIRONMENTS

St. Catherines Island possesses all of the intertidal environments that typify a mid-

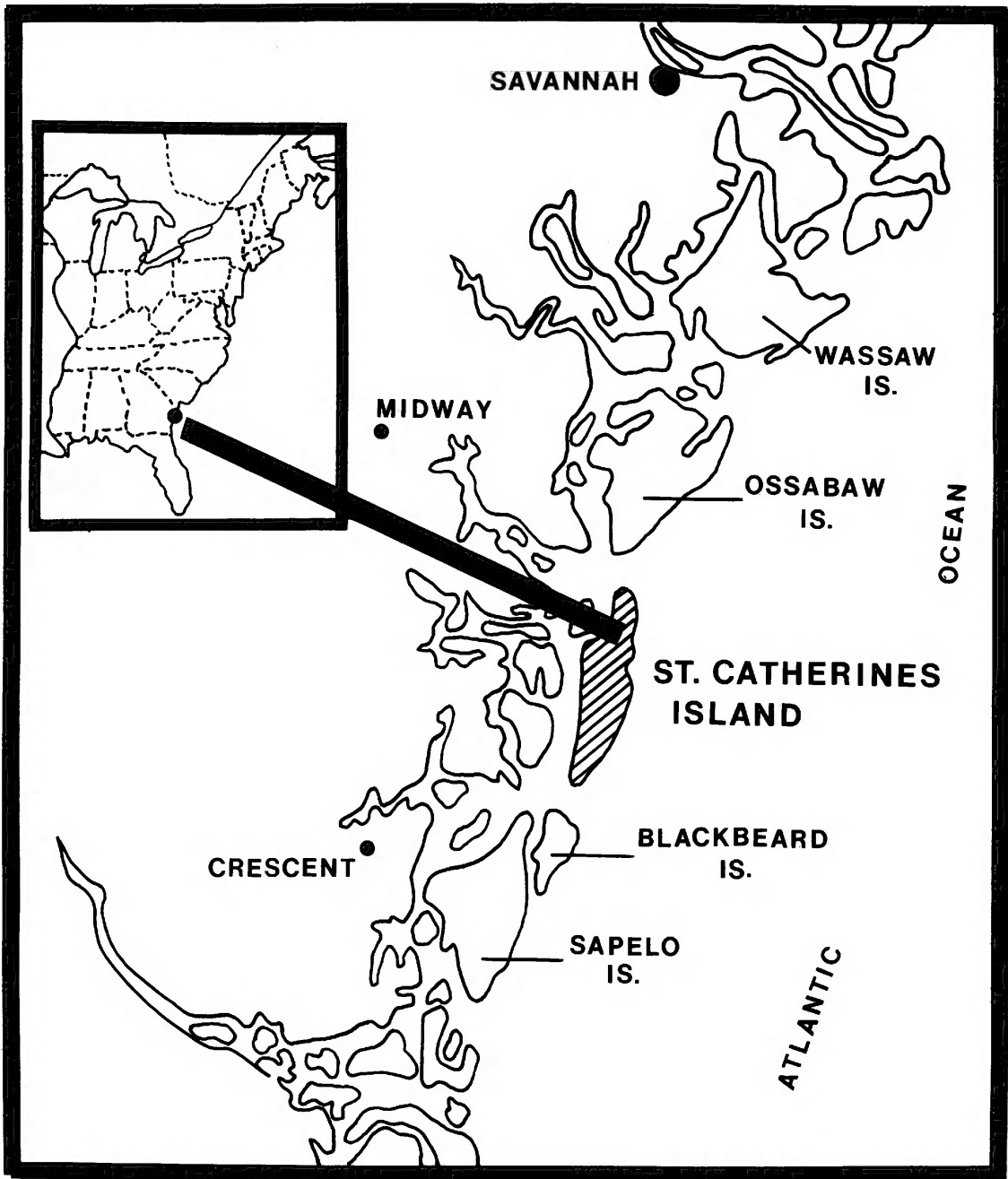


Fig. 2. Map showing the location of St. Catherine's Island, Georgia (after Morris and Rollins, 1977).

Atlantic coast barrier island system. These include sandy beaches, tidal flats, relict salt marsh deposits along eroding beaches, and active salt marshes (fig. 4).

SANDY BEACHES: In general, the littoral beaches of the sea islands of Georgia have

the finest grain size and lowest calcium carbonate content of any beaches along the southeastern coast of the United States (Giles and Pilkey, 1965). These beaches are further characterized by slopes less than 2° , extensively developed ridge and runnel systems



Fig. 3. Aerial photograph of St. Catherine's Island, Georgia.

weakly developed berms, frequent foreshore, backshore and dunal concentration of heavy minerals, and conspicuous wrack lines of shell material and fragmented marsh grass flushed from tidal creeks and mobilized by littoral transport (Howard and Frey, 1980).

The sandy beaches of St. Catherine's Island are mainly restricted to the Atlantic (eastern) side. Most of the shoreward expanse of this beach consists of massive wave-cut bluffs on the flanks of eolian dunes. In areas where dunes are not prevalent, narrow low-barrier ridges, promulgated and modified by eolian and storm processes, are situated immediately behind the high water mark and separate the ocean from areas of marsh development. The barrier ridge is occasionally breached by washover fans which develop during storms in association with relict marsh features and/or active spits (Howard and Frey, 1980; Deery and Howard, 1977). The most prominent development of massive eolian dunes is at station 7 and along the south beach area between Flag Pond and McQueens Inlet (fig. 4). The area south of station 8 to McQueens Inlet has extensive development of salt marshes behind low beach ridges.

TIDAL FLATS: The tidal flats along the Georgia coast are closely associated with beaches, commonly protected by inlet shoals or spits (Howard and Frey, 1980). The Cabretta and Nannygoat tidal flats of the Sapelo Island area have received a great deal of study, primarily dealing with preservable sedimentological and biological features (Howard and Dorjes, 1972). Such protected tidal flats are depositional sites of fine-grained organic-rich detritus which supports abundant and diverse mud-ingesting organisms. Low-amplitude ripple marks regularly carpet large expanses of the tidal flats. Abundant dark-colored fecal material becomes entrained in the ripple troughs, accentuating the patterns of ripple fields. Biogenic processes predominate in the tidal flats, creating a myriad of bioturbational features (Howard and Frey, 1980; Morris and Rollins, 1977).

On St. Catherine's Island sandy tidal flats are most extensively developed at stations 5 and 6, at the northeastern point of the island. They were conspicuously wide (500–600 ft at low tide) during the late 1970s but are now greatly restricted due to a changed configuration of the large sand spit immediately to the south (Morris and Rollins, 1977, fig. 23). The faunal elements of these tidal flats were discussed in detail by Morris and Rollins (1977) and are dominated by the tubicolous

polychaetes *Diopatra cuprea* (Bosc) and *Onuphis microcephala* Hartman and the acorn worm *Balanoglossus* sp.

RELICT SALT MARSHES: Old marsh muds are occasionally exhumed along erosional beaches of the Georgia coast, especially where washover fan development is active (Howard and Frey, 1980). The east-central portion of St. Catherines Island, near Seaside and McQueens Inlets, has been the locus of extensive barrier washover and exposure of relict mud deposits (Morris and Rollins, 1977; Deery and Howard, 1977; Pemberton and Frey, 1985). Relict mud deposits indicate former active marshes in back-barrier environments during the Holocene. Molluscan shell material recovered from relict marshes on Cabretta Island has been radiocarbon dated from 500 to 1000 B.P. (Howard and Frey, 1980) and a maximum date of 1040 B.P. was obtained from oyster shell material recovered in growth position at station 7, St. Catherines Island (fig. 4). The relict muds afford unusual opportunity for viewing salt marsh ecology and developmental history, unhampered by the often impenetrable vegetation of a living marsh, while providing a three-dimensional (i.e., stratigraphic) perspective (Rollins and Morris, unpub.). The relict deposits provide, as well, unusual intertidal habitats for modern organisms (Frey and Howard, 1969; Morris and Rollins, 1977; Frey and Basan, 1981; Pemberton and Frey, 1985).

SALT MARSHES: The *Spartina* marshes of the Georgia coastal islands are the most expansive of the area's intertidal environments and typically are developed between neap mean high water and spring mean high water tidal positions (Frey and Basan, 1978). As noted by Howard and Frey (1980), Georgia salt marshes are quite unlike those in Europe. They do not represent the thick accumulations of rather static basinfill, but are, instead, thin sequences which are the products of a dynamic, laterally migratory facies complex, more analogous to fluvial systems. Georgia marshes, unlike those of the North Sea, have abrupt lower boundaries usually formed by tidal channel banks and levees. Tidal flushing of North Sea marshes marches directly across broad tidal flats, but, in Georgia marshes, tidal water exchange must usually follow a circuitous route through a maze of small tidal

creeks (Howard and Frey, 1980). This affords a lower energy, more sheltered marsh setting. Small fringing marshes which abut large tidal channels of the Georgia coastal islands represent higher energy environments and are closer analogs to the North Sea marshes. The microenvironments of Georgia marshes have been ably discussed by Basan and Frey (1977), based on detailed study of marshes in the vicinity of Sapelo Island. These habitats include creek banks, low marsh (divisible into six smaller habitats), transitional marsh, and high marsh (with five subdivisions).

Macrophytes are the dominant organisms of Georgia marsh habitats, except in tidal creek channels, the mud barrens of the low marsh, and the sand barrens of the high marsh. The marsh cordgrass, *Spartina alterniflora*, dominates the low marsh, the transitional marsh, and the lower portions of the high marsh. A variety of macrophytes populate the remainder of the high marsh. Burrowing macroinvertebrates (e.g., the decapods *Uca* spp., the mud snail *Ilyanassa obsoleta*, and several polychaetes) are most diverse along creek banks. In fact, fiddler crabs and polychaetes comprise the densest populations of macroinvertebrates in Georgia salt marshes (Basan and Frey, 1977). Molluscs are most abundant in low-marsh areas where there are frequent dense populations of the ribbed mussel *Geukensia demissa* (Dillwyn) and the marsh periwinkle *Littorina irrorata*. Other molluscs (i.e., the oyster *Crassostrea virginica* (Gmelin), the hard shell clam *Mercenaria mercenaria* (Linné), the mud snail *Ilyanassa obsoleta*, the brackish marsh clam *Polymesoda caroliniana* (Bosc), the stout razor clam *Tagelus plebeius* (Lightfoot), and the pulmonate snail *Melampus bidentatus*) have very patchy distributions associated with specific marsh habitats. Teal (1962) tabulated 95 terrestrial and aquatic invertebrate species in Georgia salt marshes and Basan and Frey (1977) claimed that only 17 of these species are limited to the salt marsh while, in contrast, approximately 270 species of macroinvertebrates can be found in beach and shelf environments off Sapelo Island (Dorjes, 1972). The microfauna of Georgia salt marshes has, to date, received minimal attention (Goldstein and Frey, 1987). The marsh ostracodes and foraminifera of St.

ST. CATHERINES SOUND

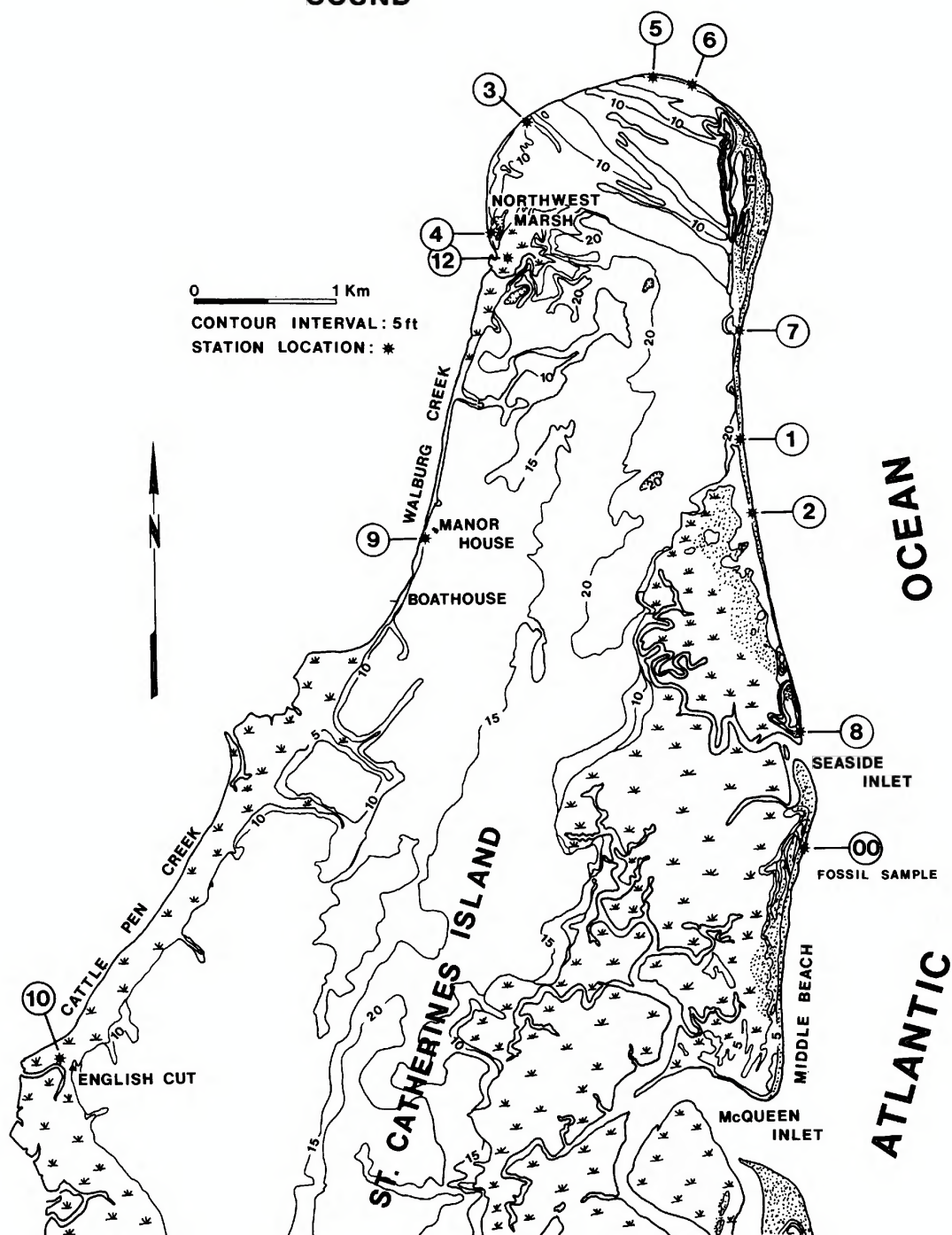
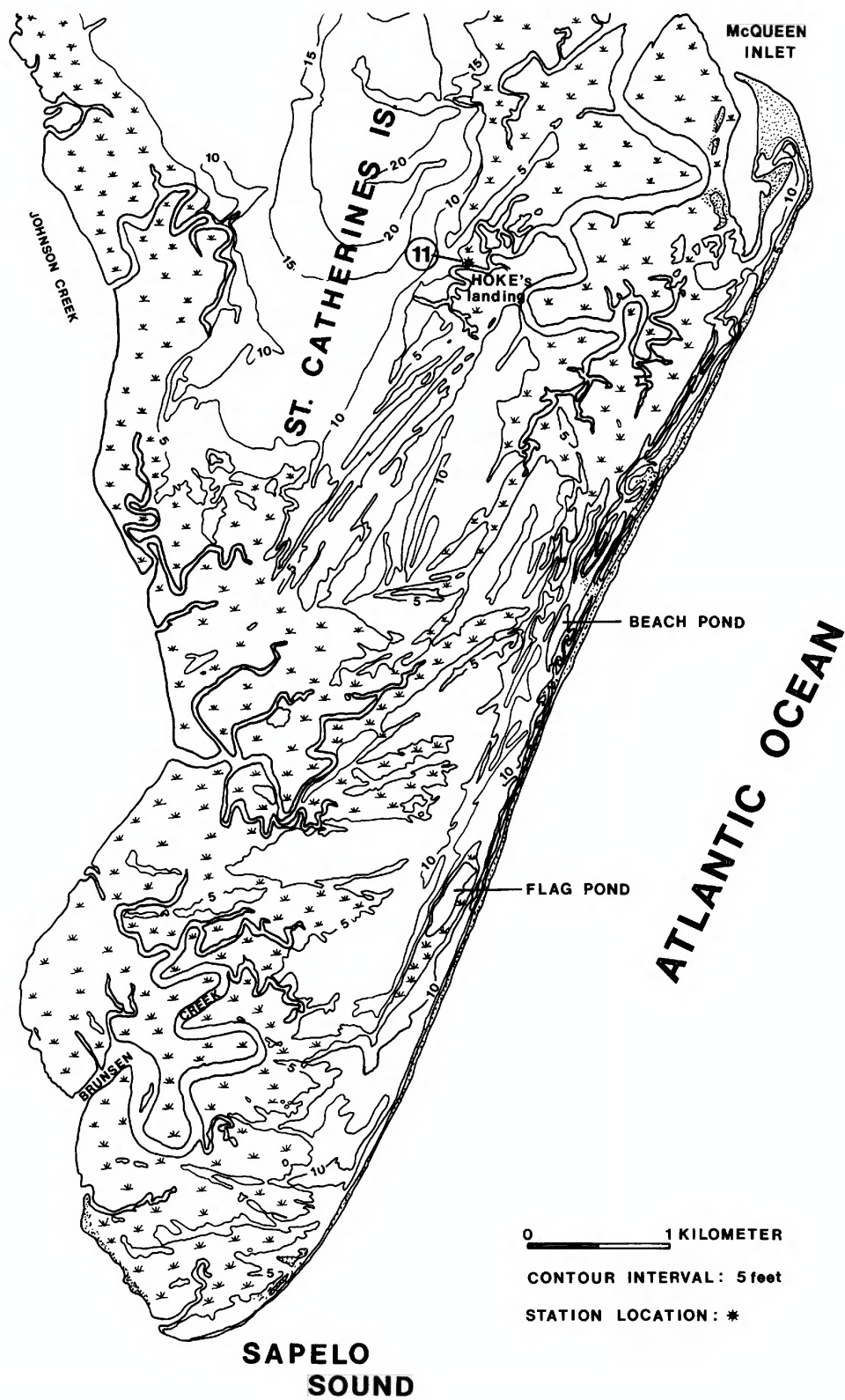


Fig. 4. Topographic map of St. Catherine's Island, Georgia, showing location of sample stations.



Catherines Island are currently under study, however (C. Venn, personal commun.).

The salt marsh environments of St. Catherines Island are numerous and extensive (fig. 4). Several of these served as collection sites for populations of *L. irrorata* used in this study and these sites are described in the next section.

FIELD METHODS

Populations of *L. irrorata* were sampled at four salt marsh localities on St. Catherines Island. These are designated as stations 9, 10, 11, and 12 on figure 4. For each station at least two 1.5×3.0 m grids were established. The grids were bounded by stakes and string. To facilitate counting and collecting, additional strings were used to divide the grids into octants. Gastropods positioned directly on the perimeters of the grids were included in the study. Gastropods were often found climbing on the grid stakes and, in such cases, if the snails were situated toward the inside of the grid perimeters, they were counted or collected; snails situated on the outside stake surfaces were disregarded. At English Cut (station 10), three grids were utilized in an attempt to minimize sampling error due to low population density. At each station one grid was treated as a control and the other used for sampling. Each control grid was monitored on an average of every two days for a three-week period in June 1976. At the control grids, each octant was counted separately and special care was taken to observe both sides of *Spartina* blades for "hidden" snails. The number of snails in each octant was recorded separately; thus the final tally in each control grid was a sum of eight numbers. This technique permitted observation of the degree of "patchiness" of *L. irrorata* over the entire grid. During each visit, a census of *L. irrorata* was taken to ascertain short-term changes in population size. The sampling grids were also monitored every two days, at which times all the *L. irrorata* specimens were collected from inside the grid margins. This approach was adopted in order to (1) gather information concerning the short-term repopulation of these sites and its relationship to the size, age, and motility of the gastropods and (2) collect, under sufficiently

controlled conditions, population samples to be used in subsequent morphometric analysis. The sampling grids were subdivided in the same manner as the control grids. Each octant was carefully scrutinized to insure collection of every snail. Collected specimens were placed in plastic bags and later preserved with buffered formalin in glass jars.

Station 9 (Manor House locality) is a small fringing marsh located on the western side of the island adjacent to Walburg Creek and near the island's research compound (see fig. 4). At the grid locations the marsh is only 4 to 6 m wide, from mean high water to mean low water and the shoreward margin of the marsh abuts a 2 m high terrace marking the erosional edge of the island's Pleistocene core. This marsh is more exposed to tide and storm activities because it is directly adjacent to a wide channel, Walburg Creek (actually, a dredge-maintained portion of the intracoastal waterway). It lacks the protection of a natural levee and the buffering effect of small labyrinthine tidal creeks. *Spartina alterniflora* averages no more than 0.5 m high, corresponding to Kuenzler's (1961) category of "short *Spartina*." Dominant macroinvertebrates at station 9 are *Littorina irrorata*, *Geukensia demissa*, and *Uca* spp.

Station 10 (English Cut) is part of a large salt marsh which extends along the western margin from the southern tip northward to about $\frac{1}{2}$ km of the compound area (fig. 4). This marsh is narrowest a few hundred meters north of station 10 and widest along the southern third of the island where it almost reaches across the entire island. The control grid at station 10 was positioned 34 m from a U.S. Coast and Geodetic Survey benchmark along an azimuth of N 50 W. The two collecting grids were 10 m north and 10 m south of the control grid. All grids were in a short *Spartina* back-levee marsh and the dominant faunal elements were *L. irrorata*, *Geukensia demissa*, *Uca* spp., and, anomalously, a few *Polymesoda caroliniana* individuals. The latter appear to reflect brackish conditions from freshwater runoff at English Cut.

Station 11 (Hoke's Landing) is situated at the inner edge of an extensive salt marsh on the eastern side of the island. This marsh extends approximately 7 km along the is-

TABLE 1
Mean of Measured Parameters, Per Station^a

Station	TH	TW	HA	WA	R	Y	N
Manor House 9	14.58	10.28	9.23	6.96	4.03	8.43	233
English Cut 10	16.95	12.32	11.24	8.02	4.87	8.54	158
Hokes Landing 11	15.33	11.10	9.84	7.14	4.51	8.60	209
Northwest Marsh 12	15.39	11.07	9.76	7.32	4.51	8.72	124
Fossil 00	14.54	11.05	9.44	6.70	4.24	7.90	89

^a TH = total height, TW = total width, HA = height of aperture, WA = width of aperture, R = radius of the last whorl, Y = height of the last whorl, and N = the number of specimens measured.

land's eastern coast and achieves a maximum width of about 2 km. Station 11 was established near a moderately large tidal creek and the control grid was positioned 30 m north of an old boiler and 17.5 m north of a cement drain pipe. The station also represents a short *Spartina* back-levee setting, but one which is transitional to a high-marsh environment. Thus, the substrate at station 11 was drier and coarser in texture than at the other stations. Macrofaunal components were not different, however, and were dominantly *L. irrorata*, *Geukensia demissa*, and *Uca* spp.

Station 12 (Northwest Marsh) was established in a small salt marsh adjacent to Walburg Creek in the northwest corner of the island. The marsh is about 1 km long by 200 m wide and the control and sample grids were placed in the center of the marsh, approximately 35 m north of a small tidal creek which bisects the marsh (fig. 4). The setting was typically low, wet back-levee marsh and major macrofaunal components were identical to those of the other stations.

The relict marsh fossil sample of *L. irrorata* (N = 89) was collected on Middle Beach, between McQueen and Seaside Inlets. We collected only those snails partially exposed by erosion on the beach surface. Most likely, smaller snails had been winnowed from the surface of the relict mud by continued wave action.

MORPHOMETRIC ANALYSIS

Several weeks after collection, the snails were removed from the formalin, washed, and placed in 90 percent ethyl alcohol to prevent deterioration and to facilitate handling.

Specimens were measured using both a Leitz binocular microscope equipped with an

ocular micrometer and Yuasa vernier calipers. The calipers were used for the largest snails and they were calibrated and checked for accuracy by using a Leitz 2 mm stage micrometer. The accuracy of both methods was within 0.01 mm.

Eighteen parameters were measured (fig. 5), following a method employed by Newkirk and Doyle (1975). The values R1 and H1 were, however, taken on the first measurable whorl. Often specimens had only four or five measurable whorls and, in such cases, remaining measurements up to whorl six were assigned zero values and later interpreted by the computer as missing data. No snail was found to have more than six whorls. Table 1 summarizes values of measured parameters and sample sizes at each sample station.

Several morphological parameters were calculated from the 18 measurements. We calculated three of the parameters of coiled shells developed by Raup (1966), using techniques similar to those of Newkirk and Doyle (1975).

The parameter T was defined as the ratio of change in Y with respect to R (fig. 5). The equation $T = Y/R$ gives results similar to those of Thompson (1952) and Vermeij (1971) and provides values approximately one-half those derived by Raup (1966). The parameter T provides an indication of whorl translation (or relation of shell height to shell width).

The equation $S = WA/HA$ was used in this study to ascertain the shape of the generating curve (S). This provides a crude index of the shape of the aperture, for when the value of S is 1, the aperture is circular. Vermeij (1971) used an inverse S function ($S = HA/WA$) which provides values greater than 1.0 for apertures with height larger than width. Most

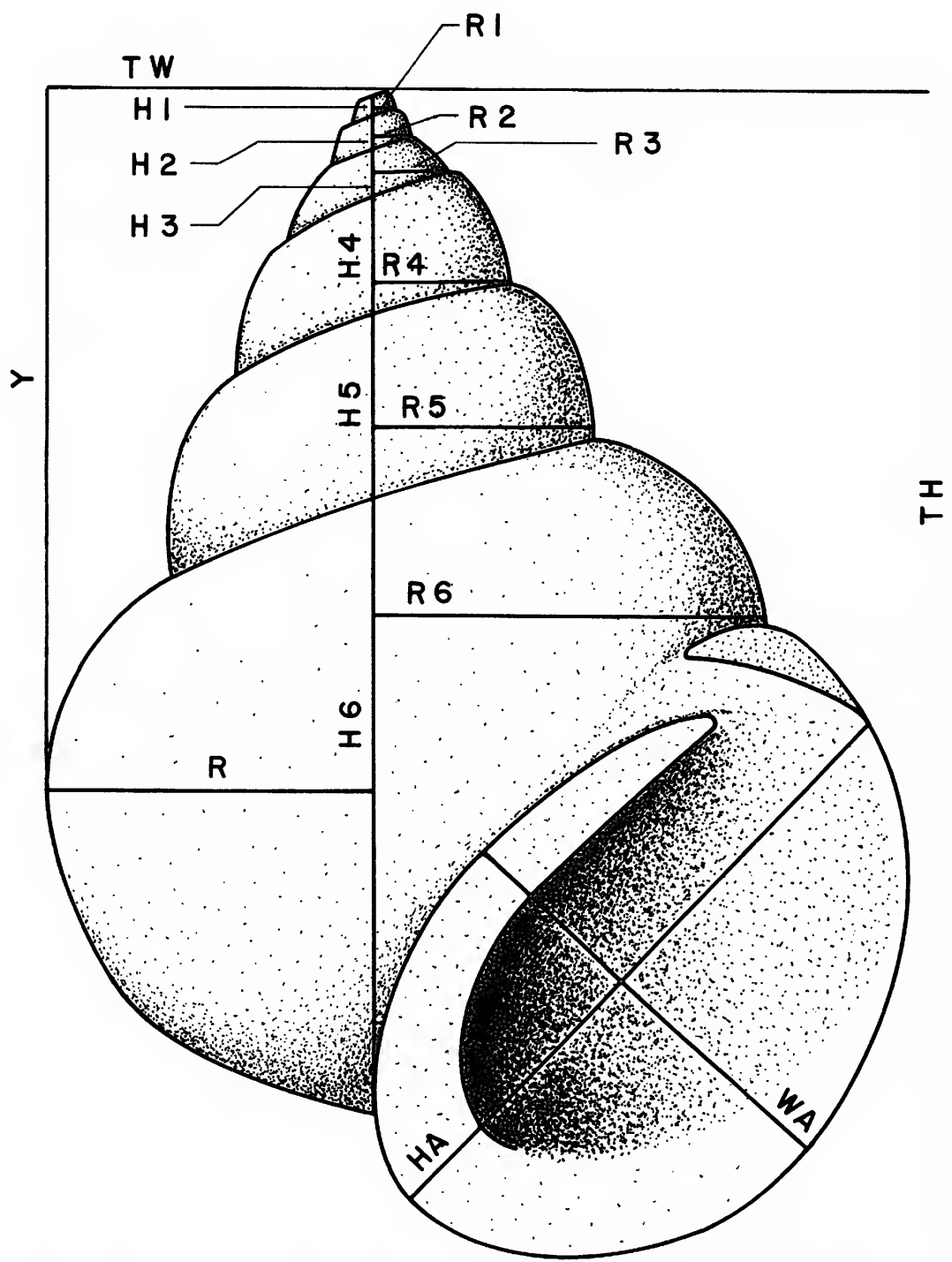


Fig. 5. Schematic representation of a *Littorina irrorata* shell showing the 18 shell measurements used in this study. TH = total height; TW = total width; HA = height of aperture; WA = width of aperture; R = radius at aperture margin; Y = height from last whorl; H1 = height of 1st whorl; R1 = radius of 1st whorl; H2 = height of 2nd whorl; R2 = radius of 2nd whorl; H3 = height of 3rd whorl; R3 = radius of 3rd whorl; H4 = height of 4th whorl; R4 = radius of 4th whorl; H5 = height of 5th whorl; R5 = radius of 5th whorl; H6 = height of 6th whorl; R6 = radius of 6th whorl.

of the *L. irrorata* specimens measured in this study had S values slightly larger than 1.0, indicating that the height of the aperture was larger than the width.

The Raupian parameter W is the ratio of the radius of a point on one whorl to the radius taken at the corresponding point on the previous whorl. This value, then, estimates the whorl expansion rate, or the rate of increase in shell radius from one whorl to the next. Gastropods do not always possess constant whorl expansion rates. They often display ontogenetic changes in W, so an examination of the radius of a whorl to the preceding one could give results that would be atypical for the entire shell. Thus, in this study, an alternative method of calculating W was used in which the calculated value was an average of the whorl expansion rate. The equation used was:

$$W2 = (\Sigma Rn + 1/Rn)/N - 1$$

where n is a numbered whorl, N is the number of whorls, and R is the radius. This equation was used to provide a meaningful ontogenetic average value for whorl expansion rate. A comparison of this equation with the one suggested by Newkirk and Doyle (1975), $W = Rn/Rn - 1$, demonstrated a poor correlation (between 2 and 10%). The values of W2 were, on the average, higher than those of W. This was due to lower whorl expansion rates in the juvenile and adult whorls of *L. irrorata* compared to higher whorl expansion rates in growth stages transitional between juvenile and adult. W2 proved to be as statistically valid as W.

Raup (1966) also developed a parameter (D) which is the position of the generating curve relative to the axis of coiling. In *L. irrorata* the inner margin of the whorl is always in contact with the coiling axis. Thus D is always zero and was not calculated in this study.

Vermeij (1971) derived a parameter (E) which relates the position of the plane of the aperture to the coiling axis. The value E is defined as the smallest angle between the axis of coiling and the plane of the generating curve, or, in a functioning gastropod, the angle of elevation of the coiling axis. Vermeij (1973) used a small reflecting goniometer to calculate the value of E. Linsley (1977) de-

veloped a similar parameter and discussed the functional significance of such parameters in motile gastropods.

We utilized three methods in attempts to obtain values of E for *L. irrorata*. The first method was similar to the technique of Vermeij and a small goniometer was constructed to directly read the values of E. This was applied to several small population samples, but because the whorls of *L. irrorata* translate about 30°, E was often difficult to precisely measure by this method. In an attempt to calculate E directly from size measurements, two equations:

$$EF = \sin R[1.0/(HA/R(N))] \times 100$$

and

$$EF2 = \cos D\{1.0/[(HA^2 + TH^2) - (2HA \times TH)]/r^2\}$$

where sin R is the sine in radians and cos D is the cosine in degrees, were derived in order to solve EF using the laws of a right triangle and EF2 using the laws of sines. The three methods were compared and E and EF exhibited about 60 percent correlation, but correlations between E and EF2 and between EF and EF2 were very poor. EF values were higher than the values of E, because EF does not take into account the amount of whorl translation. In this morphological analysis, we determined that EF would be the most suitable indicator of aperture angle.

DISCUSSION OF RESULTS

UNIVARIATE ANALYSIS

The data set of thousands of measurements generated by this study were treated to standard statistical analysis as outlined by Imbrie (1956). The mean, standard deviation, coefficient of variation, and standard error were calculated for each measured variable, for each day's collection at individual stations, the total collection at each station, and for all the specimens collected at all stations. In no case did the standard error of the mean exceed 0.30. We checked the stability of measurement technique by individually measuring a small population sample and a comparison of means revealed variation of no more than 0.04 mm for any parameter. Univariate analysis yielded several results:

TABLE 2
Mean of Measured Parameters for Each Day's Collection^a

Identifier	TH	TW	HA	WA	R	Y
76096081	15.91	11.31	10.13	7.65	4.44	9.32
76096201	11.94	8.24	7.42	5.59	3.22	6.65
76106161	16.80	11.92	10.86	7.71	4.90	8.26
76106181	13.63	10.21	9.07	6.19	4.43	7.24
76106211	15.70	10.76	10.22	7.95	5.07	8.13
76106231	**	**	**	**	**	**
76106251	**	**	**	**	**	**
76106271	15.16	10.93	9.95	7.02	4.53	7.82
76106162	18.17	13.06	11.96	8.67	5.20	9.07
76106182	16.76	12.44	11.25	7.88	4.42	8.32
76106212	17.95	13.03	11.97	8.55	4.93	8.74
76106232	16.41	11.91	10.99	7.97	5.35	9.06
76106252	16.62	12.56	11.17	7.82	4.64	8.33
76106272	16.22	11.76	10.83	7.72	4.51	7.98
76116161	15.99	11.72	10.27	7.54	4.85	9.19
76116181	14.40	10.56	9.33	6.67	4.17	7.93
76116211	16.10	11.59	10.23	7.59	4.51	9.33
76116231	15.10	10.79	9.83	7.00	4.78	8.21
76116251	13.49	9.09	8.48	5.48	4.48	6.79
76116271	13.55	9.83	8.92	6.47	3.75	6.57
76126201	15.98	11.54	10.09	7.66	4.45	9.28
76126241	14.55	10.18	9.21	6.86	4.78	8.08
76126261	13.89	10.41	9.08	6.44	4.26	6.99
76000000*	14.54	11.05	9.44	6.70	4.24	7.90

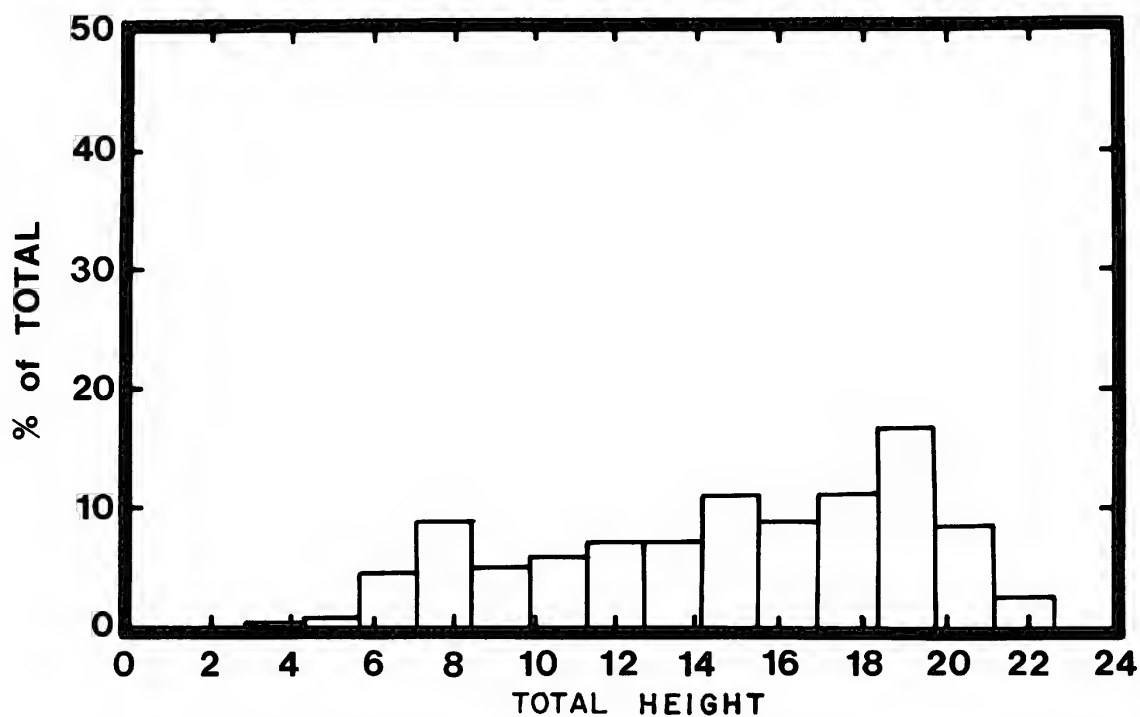
^a The first two digits of the identifier refer to the year collected, the second two digits represent the station, the next digit is the month, the next two indicate the day, and the last digit is the grid number. ** indicates insufficient data for calculation of the mean. * indicates fossil population sample.

1. Composite grouping of the data at each station showed that the mean sizes (variables TH, TW, HA, and WA) of *L. irrorata* were the smallest at station 9 and the largest at station 10 (see table 1).

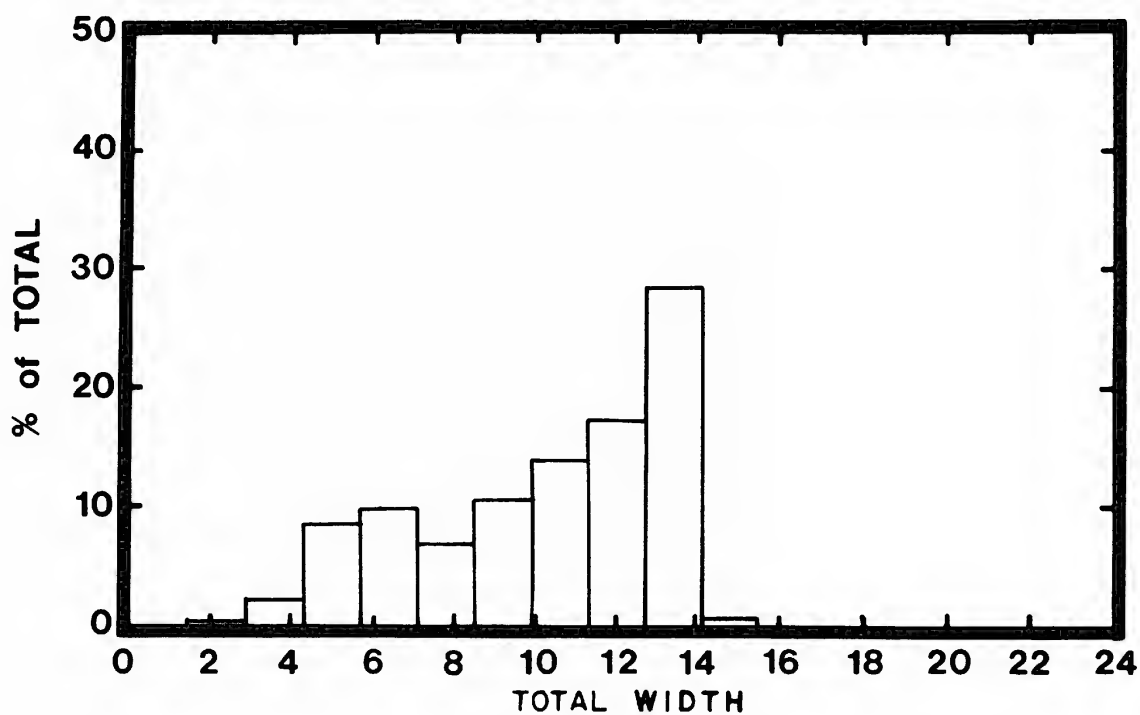
2. Analysis of each day's collection revealed that the mean size of harvested *L. irrorata* decreased at every station throughout the collecting period (see table 2). This cannot be attributed to an inverse relationship between individual size and population density, as all visible specimens were collected with each harvest. Clearly, smaller specimens entered the grid perimeters after harvesting. This may indicate that the smaller (younger) specimens of *L. irrorata* are more motile, better colonizers, and/or perhaps less territorial than the larger (adult) specimens.

It might also suggest the exclusion of the young by the adults (i.e., competition) or even differential predation. The latter is unlikely, however, for the primary predator of *L. irrorata* in Georgia salt marshes is the immature female or small adult blue crab *Callinectes sapidus* which generally selects snails less than 15 mm in shell length (Hamilton, 1976). The motility of juvenile *L. irrorata* has never been rigorously investigated, due to difficulty of tagging small specimens (Hamilton, 1978). We suspect, but cannot substantiate, that the temporal decrease in individual size noted at our collecting stations reflects greater juvenile motility in this species.

3. Histograms of measured variables were compiled for each station in order to determine the most reliable parameter to use for estimation of size and age distribution in *L. irrorata* populations. Total width proved to be a much better indicator of population structure than total height (compare fig. 6a and 6b). Measurement of total height is relatively less accurate due to abrasion and/or solution of the early whorls of *L. irrorata*. Histograms showing frequency distribution of total width displayed unimodal to weakly bimodal patterns with expected peaks in the adult size range, a typical pattern for marine macroinvertebrate populations (Olson, 1957; Craig and Oertel, 1966). We conclude that gastropod survivorship curves, which show the mortality rate of a given population, might best be constructed on total width. Smalley (1958), using shell height, illustrated a bimodal distribution of *L. irrorata* populations from Sapelo Island, but the second mode involved an abundance of specimens less than 3 mm in length. Stiven and Kuenzler (1979) also used shell width for construction of size frequency distribution histograms of populations of *L. irrorata* from North Carolina salt marshes. Their histograms included only snails with total widths of at least 6 mm that were also predominantly unimodal about the adult age classes. Hamilton (1978) found populations of *L. irrorata* from the Florida Gulf to be sexually dimorphic regarding shell height. The subtle bimodality shown by some of the histograms of total width of St. Catherine's Island specimens (fig. 7A-C) might be due to sexual dimorphism, but this was not

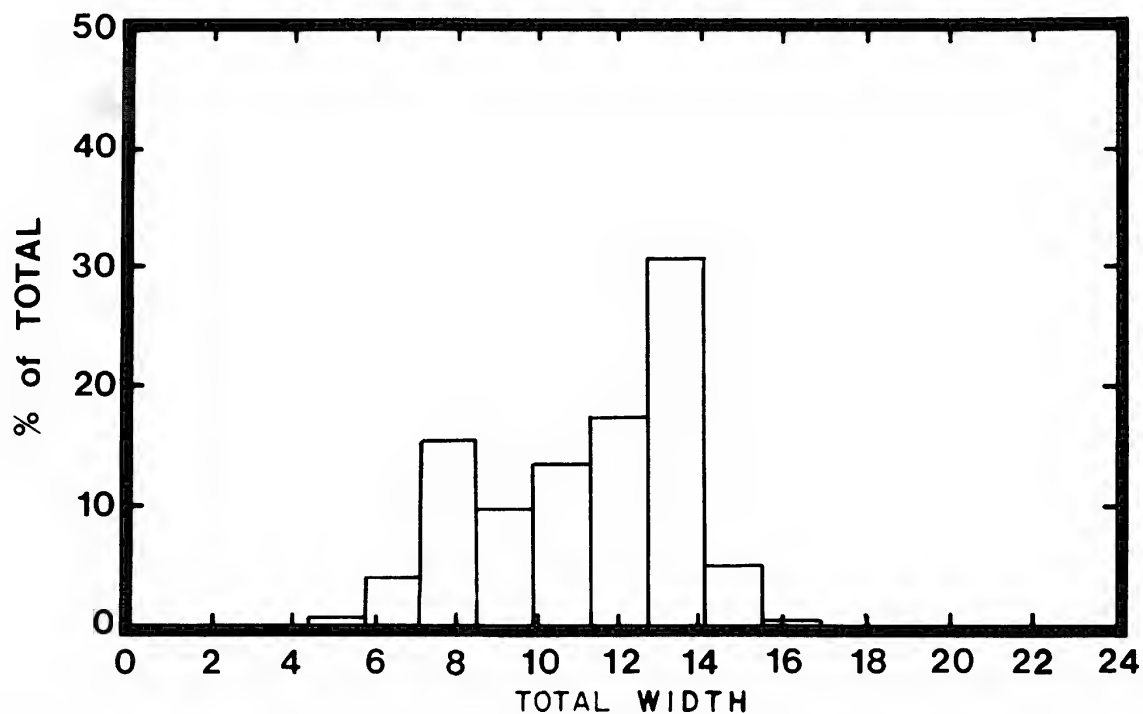


A **L. IRRORATA** **MANOR HOUSE 1976**

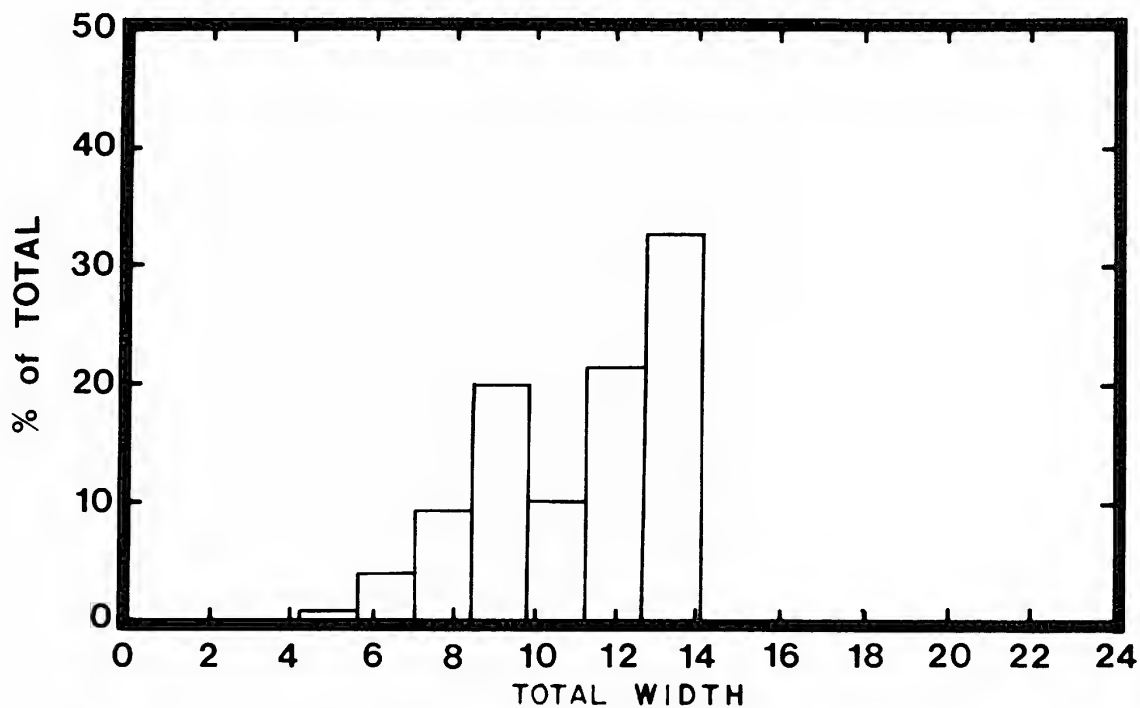


B **L. IRRORATA** **MANOR HOUSE 1976**

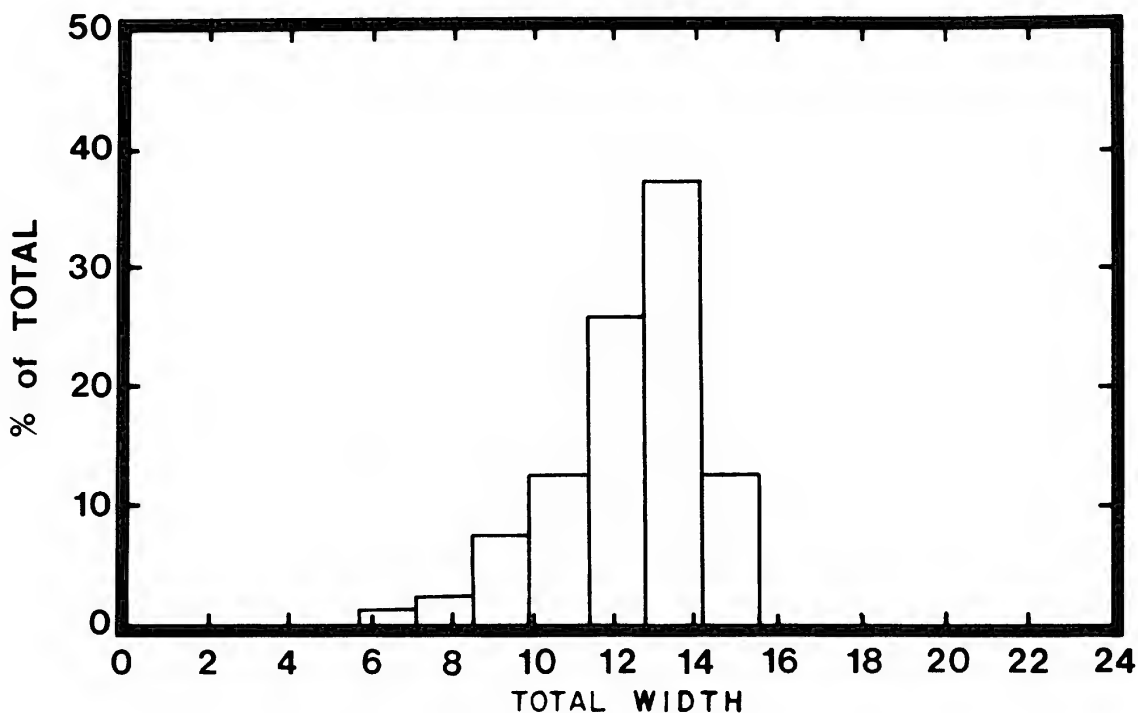
Fig. 6. Manor House cohorts (station 9): **A.** Histogram of total height of shell (TH). **B.** Histogram of total width of shell. Measurements in mm.



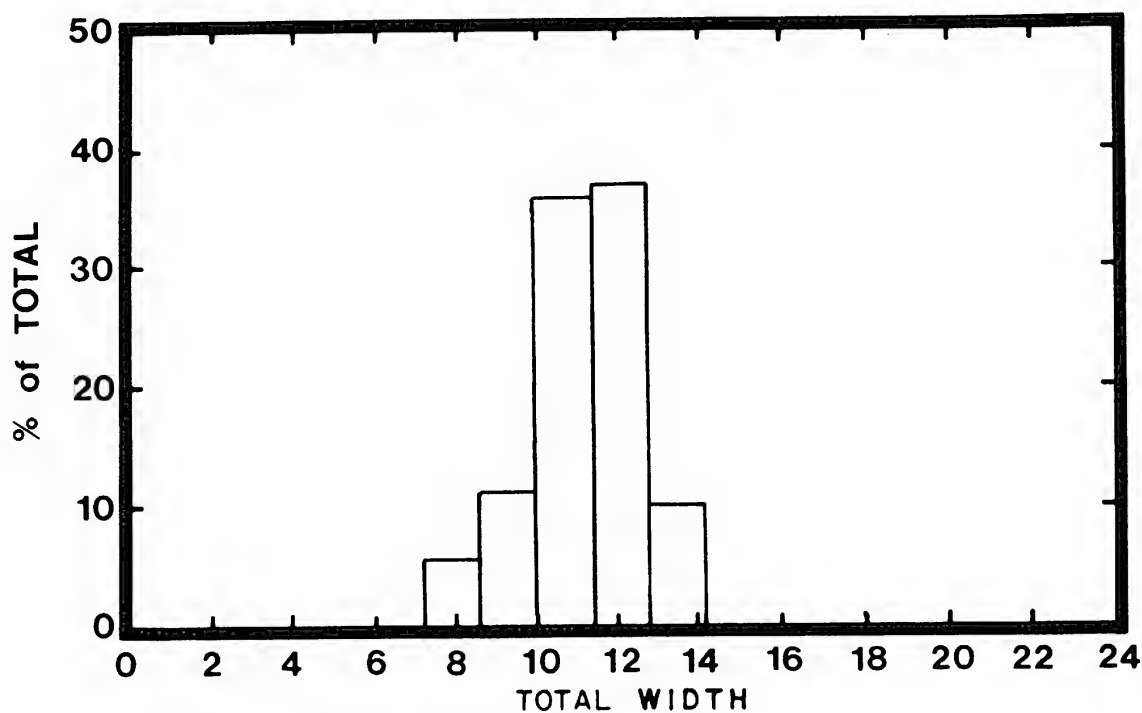
A L. IRRORATA HOKES LANDING 1976



B L. IRRORATA NORTHWEST MARSH 1976

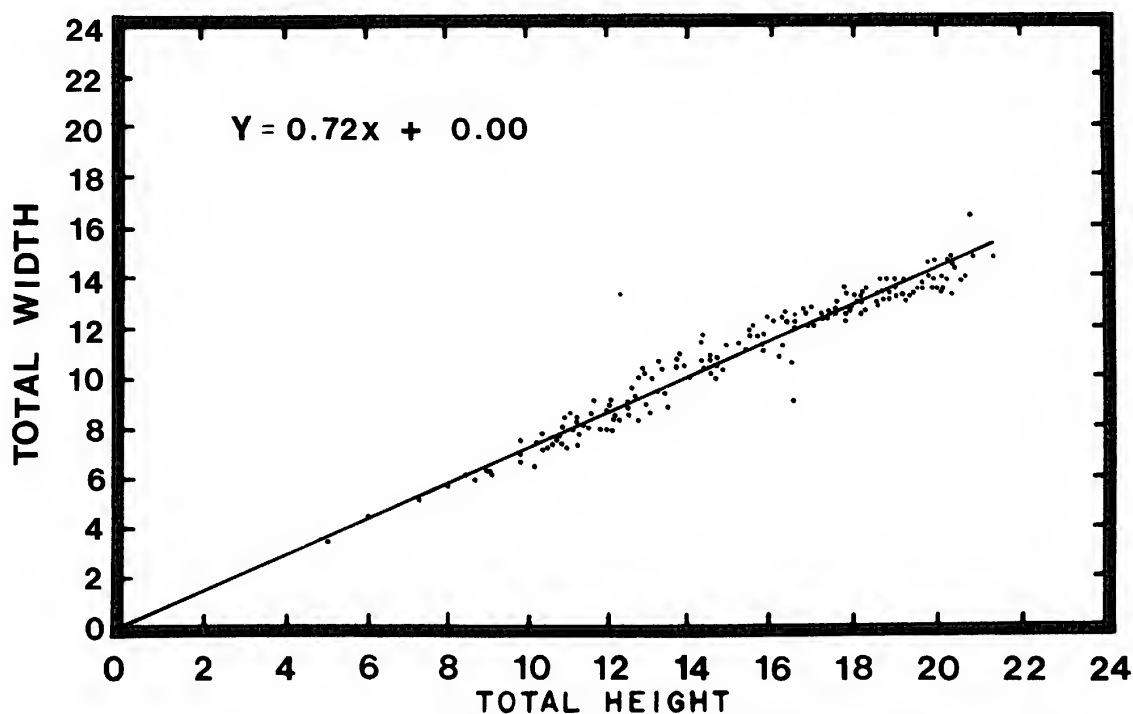


C **L. IRRORATA** **ENGLISH CUT 1976**



D **L. IRRORATA** **FOSSIL 1976**

Fig. 7. Histograms of total width (TW). **A.** Hoke's Landing (station 11) cohort. **B.** Northwest Marsh (station 12) cohort. **C.** English Cut Marsh (station 10) cohort. **D.** Fossil population. Note subtle bimodality in all of the "living" cohorts.



L. IRRORATA HOKES LANDING 1976

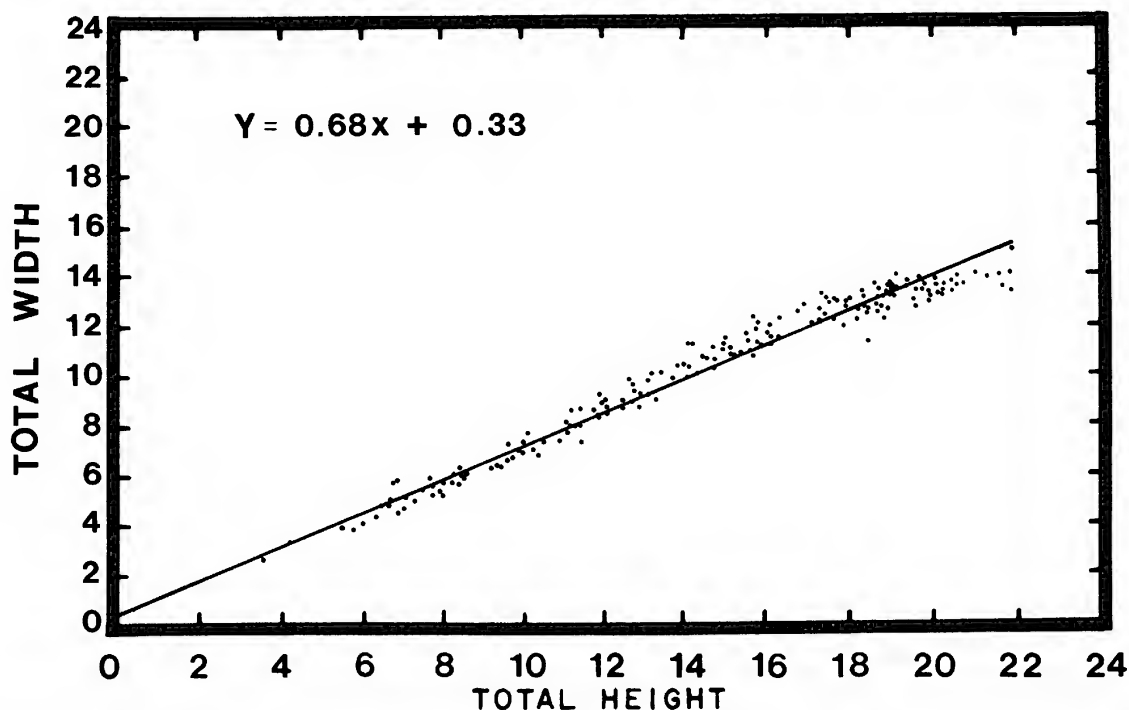
Fig. 8. Regression of total width and total height, Hoke's Landing (station 11) cohort.

confirmed since laboratory dissections were not performed.

4. Aperture area was calculated, using the formula $AR = \pi(HA \times WA/4)^2$. As was the case with the total size parameters, aperture area was absolutely highest at station 10 (English Cut) and lowest at station 9 (Manor House). However, when aperture area was normalized to avoid the obvious size dependence, the station 10 population sample possessed the lowest values and the station 9 sample had the highest. Aperture area is most likely a crude indicator of biomass, but, when normalized for shell size, might correlate with the ability of a snail to adhere to a substrate. This might further suggest that the relatively greater aperture area at the Manor House locality correlates with increased wave intensity and exposure but such simplifications are dangerous. One might also argue that aperture area should be restricted in those habitats with longer intertidal exposures due to greater likelihood of desiccation. Indeed, the

highest normalized aperture area values in this study were obtained from marsh areas which were relatively "wet." On the other hand, this pattern may reflect passive expression of a variation in some other parameter, such as translation rate (T).

5. Histograms prepared from individual whorl measurements generally showed a bimodal, or even trimodal, pattern for the earlier whorls. Whorl number 3 had a trimodal distribution for most of the measured populations. We concluded that this individual whorl multimodality was the result of abrasional and/or solutional loss of some of the earlier whorls and resultant difficulty in identification of a standard whorl (e.g., the first adult whorl). The absence of a biological shell marker such as the ontogenetic onset of a selenizone (Schindel, 1982) prevents ready whorl identification. For this reason, a computer program was devised to standardize the whorl number based on its size, with the assumption that early whorls of the same num-



L. IRRORATA MANOR HOUSE 1976

Fig. 9. Regression of total width and total height, Manor House (station 9) cohort. Note positive allometry of height in late ontogeny.

ber have generally the same size. This standardization procedure destroyed the trimodal distribution and revealed that most of the populations have six whorls as adults (91% Manor House; 94% English Cut; 77% Hokes Landing; and 73% Northwest Marsh).

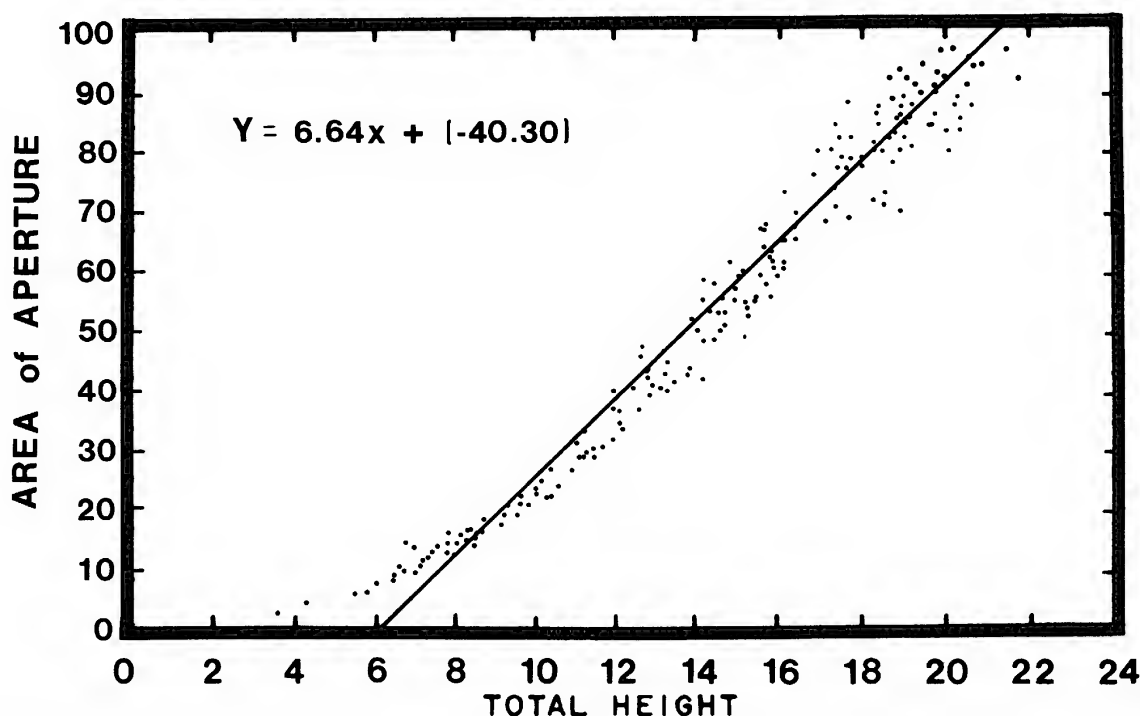
BIVARIATE ANALYSIS

The data were subjected to bivariate analysis and bivariate plots were fitted with regression lines using the reduced major axis method. This analysis included comparison of total width and total height, area of aperture and total height, width of aperture and total height, total height to last whorl and radius of last whorl, and height and width of each of the six whorls. As was the case with the histograms, the bivariate plots that involved measurements of earlier whorls generally showed the clustering of a bimodal or trimodal distribution. Normalization of whorl number removed this effect.

For all population samples, the regression of total width and total height produced straight lines with very high coefficients of correlation (e.g., fig. 8). The Manor House (station 9) sample showed a slight deflection of the regression line suggesting positive allometry of height in late ontogeny (fig. 9). Plots comparing apertural area with total shell height displayed strong positive allometry of the area of the aperture, a relationship most striking in the Manor House population (fig. 10) where many smaller individuals were available for measurement. Biomass (as indicated by apertural area) increases exponentially with respect to shell height, apparently a manifestation of area/volume constraints.

MULTIVARIATE ANALYSIS

In an attempt to gain greater insight into the morphological variation among the population samples, the data were subjected to three multivariate techniques: cluster analy-



L. IRRORATA MANOR HOUSE 1976

Fig. 10. Regression of total height and apertural area. Manor House (station 9) cohort. Note positive allometry of apertural area.

sis, factor analysis, and principal component analysis.

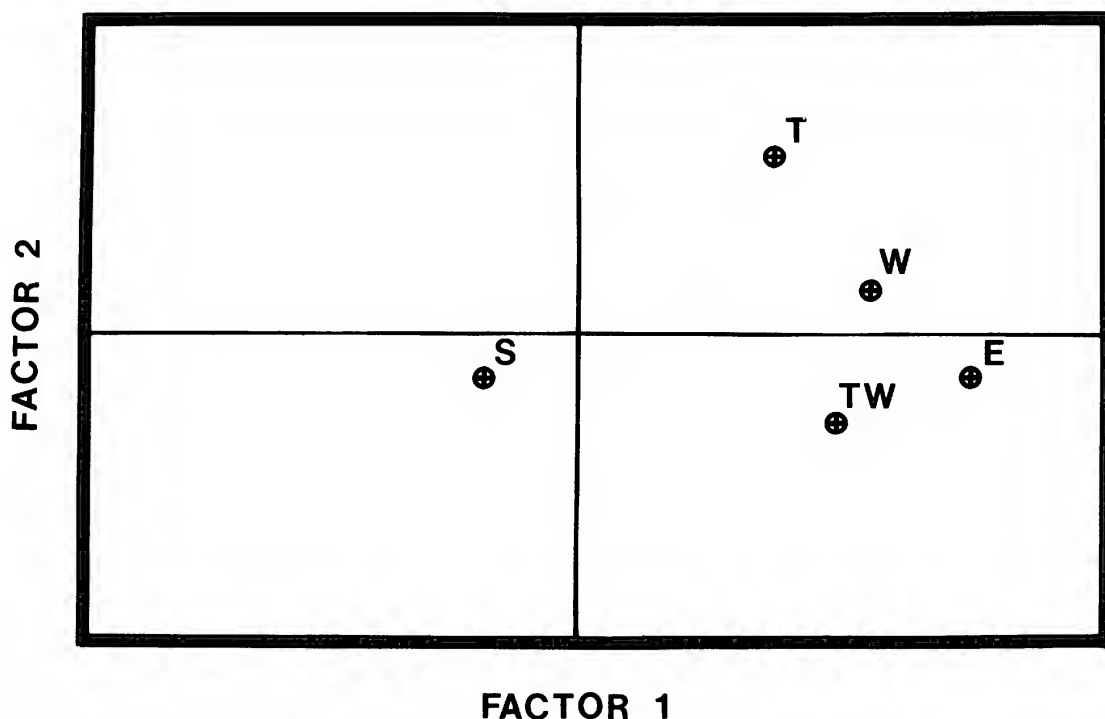
For each of the multivariate approaches, the data were analyzed in both Q-mode and R-mode. Analysis of data on cases (Q-mode analysis) was designed so that each individual represented a variable in the data matrix. In both the Q-mode and R-mode, the following variables were utilized: total width (the dependent variable), translation rate, shape (sphericity) of the aperture, whorl expansion rate, and aperture angle.

We used the cluster analysis and principal component analysis programs provided by Dixon (1975), and the S.P.S.S. factor analysis program developed by Nie et al. (1975).

The data matrix for Q-mode analysis was designed so each snail possessed a case label that designated the collecting locality, permitting assessment of morphometric variation and clustering by station. Due to the large size of the Q-mode data matrix, factor

and cluster analyses were not run on the original data. Rather, the mean was calculated for each variable in each sample and submitted to factor and cluster analysis. The Q-mode factor analysis provided eigenvalues less than 1.0 and these were not considered significant. Similarly, Q-mode principal component and cluster analyses never revealed a good separation of the data.

The factoring of the data on the individuals (R-mode factor analysis) did reveal some interesting results, including a close association of translation rate and whorl expansion rate, whereas aperture shape loaded in the opposite quadrant (fig. 11). R-mode cluster analysis showed a similar trend. Figure 11 displays all factors for all population samples, rotated orthogonally with quartimax (a simplification of the factors so that the first factor is the general one). The shape of the aperture (S) exhibited the least variation and behaved independently. Translation rate, whorl ex-



R-MODE FACTOR ANALYSIS

Fig. 11. R-mode factor analysis. Plot of factors with quartimax rotation. TW = total width, T = translation rate, S = sphericity of aperture and E = aperture angle.

pansion rate, total width, and aperture angle were mutually dependent. This suggests that the shape of the aperture might be the best parameter of *L. irrorata* for assessment of ecophenotypic change. Variation in such an independent parameter would probably more directly mirror environmental change and would be less likely "masked" by the other parameters.

DENSITY

Our study of the among-habitat variation in density of *L. irrorata* on St. Catherines Island only partially supports the work of Smalley (1958). Smalley reasoned that although *L. irrorata* might be expected to exhibit greatest abundance where there is profuse growth of *Spartina*, density is only high among the low *Spartina* grass of the high-marsh environment. Predation and tidal flushing seem to be less disruptive in the high-marsh environments. Predation of *L. irro-*

rata by the blue crab *Callinectes sapidus* is probably much more intensive than predation by raccoons and birds, and the blue crab can much more easily penetrate the stream-side and middle-marsh environments.

Average density tabulations at our control grids are recorded in table 3. The English Cut and Hokes Landing stations are clearly high-marsh, low *Spartina* habitats and averaged 6 individuals/m² and 80 individuals/m², respectively, over an 18-day period. The

TABLE 3
Average Density of *Littorina irrorata* at Station Control Grids

Station control grids	Average density/m ²
Manor House (station 9)	174
English Cut (station 10)	6
Hokes Landing (station 11)	80
Northwest Marsh (station 12)	22

TABLE 4
Density Distribution of *Littorina irrorata* From the Hokes Landing Station^a

Date	Grid 1	Control	Time and Tide
June 16		$\begin{array}{r} / \quad / \quad / \\ - \quad 163 \quad - \quad 215 \quad - \\ / \quad / \quad / \end{array} = 378$	
June 18	48(c)	$\begin{array}{r} / \ 59 \ / \ 49 \ / \ 55 \ / \ 52 \ / \\ / \ 38 \ / \ 30 \ / \ 48 \ / \ 57 \ / \end{array} = 388$	10:00 a.m., Low
June 21	62(c)	$\begin{array}{r} / \ 53 \ / \ 51 \ / \ 89 \ / \ 42 \ / \\ / \ 33 \ / \ 43 \ / \ 58 \ / \ 79 \ / \end{array} = 488$	9:30 a.m., Low
June 23	19(c)	$\begin{array}{r} / \ 55 \ / \ 55 \ / \ 56 \ / \ 55 \ / \\ / \ 32 \ / \ 29 \ / \ 51 \ / \ 67 \ / \end{array} = 400$	10:30 a.m., Low
June 25	11(c)	$\begin{array}{r} / \ 41 \ / \ 47 \ / \ 53 \ / \ 65 \ / \\ / \ 33 \ / \ 26 \ / \ 57 \ / \ 53 \ / \end{array} = 375$	11:00 a.m., Low
June 27	10(c)	$\begin{array}{r} / \ 37 \ / \ 37 \ / \ 52 \ / \ 55 \ / \\ / \ 25 \ / \ 15 \ / \ 61 \ / \ 55 \ / \end{array} = 377$	11:20 a.m., Low
June 29	4(n)	$\begin{array}{r} / \ 39 \ / \ 43 \ / \ 34 \ / \ 52 \ / \\ / \ 20 \ / \ 20 \ / \ 57 \ / \ 45 \ / \end{array} = 310$	5:00 p.m., Low
July 1	13(c)	$\begin{array}{r} / \ 38 \ / \ 39 \ / \ 55 \ / \ 70 \ / \\ / \ 32 \ / \ 25 \ / \ 58 \ / \ 57 \ / \end{array} = 374$	2:15 p.m., High
July 3	7(c)	$\begin{array}{r} / \ 38 \ / \ 28 \ / \ 37 \ / \ 42 \ / \\ / \ 28 \ / \ 21 \ / \ 54 \ / \ 58 \ / \end{array} = 306$	10:30 a.m., Low

^a A (c) indicates that the population was collected for subsequent measurement and (n) indicates that no collection was made.

Northwest Marsh station was a taller *Spartina*, middle-marsh setting and had an average density of 22 individuals/m² over a comparable interval. The Manor House station represents an exposed streamside marsh and, although no control grid was established there, contained an initial density of 174 individuals/m². We could not detect a specific pattern of density by habitat for *L. irrorata* populations in our study areas. This may reflect the small number of stations utilized in this study.

Within-habitat variation in *L. irrorata*

density predictably correlated with *Spartina* density. This relationship was clearly seen at the Hokes Landing station where the lower left portion of the control grid had sparsely developed *Spartina* grass. The density of *L. irrorata* was consistently lower in this portion of the control grid over the sampling interval (table 4).

L. irrorata density was monitored at most stations on a 2–3-day interval for a period of 18 days. Stations were visited during high as well as low tides. The Northwest Marsh and English Cut stations exhibited pronounced

TABLE 5
Density of *Littorina irrorata* from the English Cut Station^a

Date	Grid 1	Control	Time and Tide
June 16	15(c)	$\begin{array}{ccccc} / & & / & & / \\ - & 17 & - & 7 & - = 24 \\ / & & / & & / \end{array}$	7:15 a.m., Low
June 18	9(c)	$\begin{array}{ccccc} / & 7 & / & 9 & / & 4 & / & 0 & / \\ / & 5 & / & 2 & / & 2 & / & 2 & / \end{array} = 31$	9:00 a.m., Low
June 21	2(c)	$\begin{array}{ccccc} / & 6 & / & 4 & / & 5 & / & 0 & / \\ / & 4 & / & 0 & / & 0 & / & 0 & / \end{array} = 19$	9:00 a.m., Low
June 23	1(c)	$\begin{array}{ccccc} / & 6 & / & 7 & / & 4 & / & 1 & / \\ / & 5 & / & 2 & / & 1 & / & 1 & / \end{array} = 27$	9:30 a.m., Low
June 25	1(c)	$\begin{array}{ccccc} / & 5 & / & 8 & / & 8 & / & 3 & / \\ / & 6 & / & 3 & / & 1 & / & 1 & / \end{array} = 35$	10:30 a.m., High
June 27	3(c)	$\begin{array}{ccccc} / & 5 & / & 2 & / & 8 & / & 0 & / \\ / & 4 & / & 0 & / & 1 & / & 2 & / \end{array} = 22$	
June 29	4(n)	$\begin{array}{ccccc} / & 7 & / & 0 & / & 8 & / & 2 & / \\ / & 5 & / & 1 & / & 1 & / & 3 & / \end{array} = 27$	4:00 p.m., Low
July 1	4(n)	$\begin{array}{ccccc} / & 9 & / & 3 & / & 14 & / & 2 & / \\ / & 10 & / & 1 & / & 2 & / & 0 & / \end{array} = 41$	1:20 p.m., High
July 3	3(n)	$\begin{array}{ccccc} / & 6 & / & 4 & / & 7 & / & 0 & / \\ / & 5 & / & 1 & / & 0 & / & 0 & / \end{array} = 23$	9:00 a.m., Low
Date	Grid 2	Date	Grid 2
June 16	41(c)	June 18	32(c)
June 21	15(c)	June 23	15(c)
June 25	11(c)	June 27	12(c)
June 29	7(n)	July 1	19(n)
July 3	8(n)		

^a A (c) indicates that the population was collected for subsequent measurement and (n) indicates that no collection was made. Each number in the control column represents the number of individuals collected in each octant of the control grid.

day-to-day fluctuation in the density of *L. irrorata*, whereas Hokes Landing was remarkably stable. There appears to be a direct correlation between average density of *L. irrorata* at a station and short-term stability of

population size. We noted no tidal control, however, upon *L. irrorata* standing crop.

The grids which were sampled periodically throughout the study interval invariably suffered a net loss in number of individuals (ta-

TABLE 6
Density Distribution of *Littorina irrorata* at the Northwest Marsh Station^a

Date	Grid 1	Control	Time and Tide
June 20	79(c)	$\frac{\begin{array}{ccccccc} / & 11 & / & 13 & / & 9 & / & 10 & / \\ / & 9 & / & 5 & / & 2 & / & 9 & / \end{array}}{= 68}$	
June 24	31(c)	$\frac{\begin{array}{ccccccc} / & 9 & / & 14 & / & 3 & / & 6 & / \\ / & 5 & / & 3 & / & 4 & / & 9 & / \end{array}}{= 53}$	
June 26	14(c)	$\frac{\begin{array}{ccccccc} / & 14 & / & 29 & / & 6 & / & 11 & / \\ / & 17 & / & 5 & / & 5 & / & 10 & / \end{array}}{= 97}$	11:00 a.m., High
June 29	12(n)	$\frac{\begin{array}{ccccccc} / & 18 & / & 33 & / & 13 & / & 17 & / \\ / & 24 & / & 5 & / & 6 & / & 19 & / \end{array}}{= 135}$	10:00 a.m., High
July 1	35(n)	$\frac{\begin{array}{ccccccc} / & 25 & / & 31 & / & 10 & / & 19 & / \\ / & 25 & / & 6 & / & 9 & / & 11 & / \end{array}}{= 136}$	9:30 a.m., High
July 3	14(n)	$\frac{\begin{array}{ccccccc} / & 22 & / & 30 & / & 11 & / & 14 & / \\ / & 20 & / & 12 & / & 6 & / & 15 & / \end{array}}{= 130}$	12:10 p.m., High

^a A (c) indicates that the snails were collected and (n) indicates that no collection was made.

ble 5). Clearly, as mentioned by Hamilton (1978), *L. irrorata* exhibits very little short-term lateral motility. As previously noted, juveniles exhibited greater lateral movement than adults. Examination of daily collections at each station, however, reveals a few episodes of possible repopulation (see the June 29–July 1 interval at Northwest Marsh). Such a large increase in standing crop is difficult to explain in terms of errors in field count alone. After snails had been picked several times from a grid, the quantity of snails repopulating the grid leveled off. This is best demonstrated at the English Cut station where a total of six collections were made over the study interval. After the third collection at this station, density remained approximately constant. Hokes Landing station, which had a much higher density than English Cut, also displayed this equilibrium in the number of recruits. Recruitment potential seems to only crudely reflect differences in population density surrounding the harvested grids. After a few harvests, recruitment at Hokes Landing was as slow as English Cut. Possibly, cu-

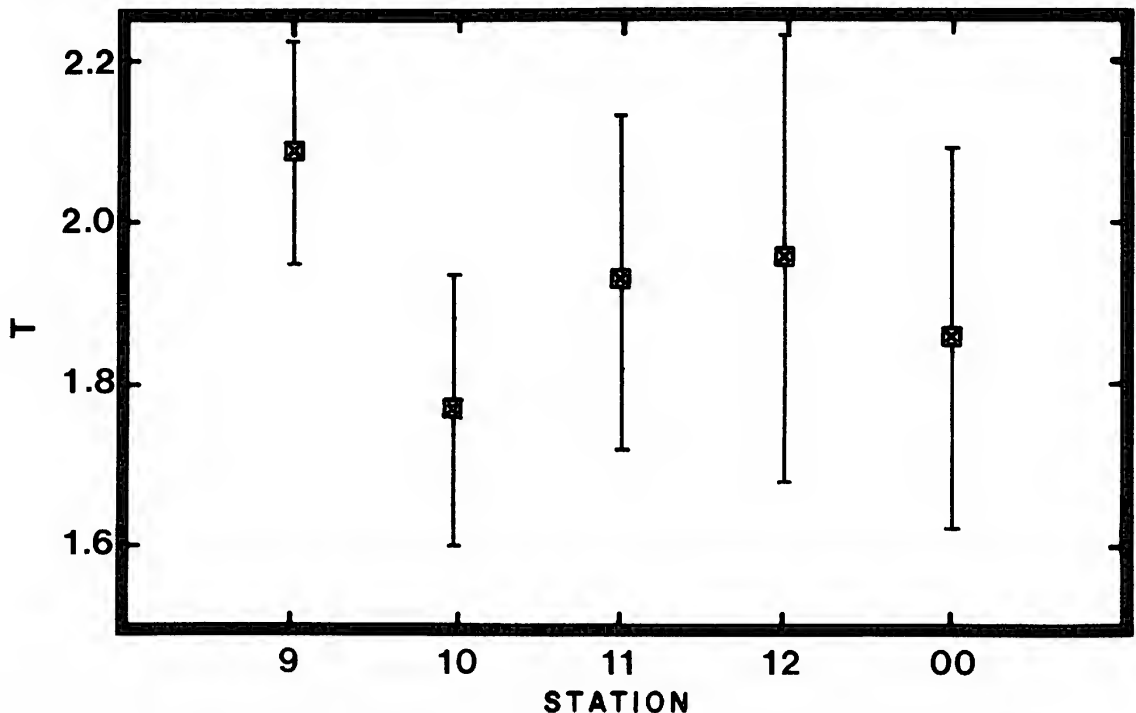
mulative disturbance of the grid peripheries (e.g., trampling of *Spartina* grass) was a factor leading to lowered recruitment at the stations.

Size was inversely related to density at the sample stations. English Cut, which had the lowest average density (6/m²) also contained the largest snails, whereas the Manor House station, with the highest density (176/m²), housed the smallest snails. This agrees with the observations of Smalley (1958), Stiven and Kuenzler (1979), and Stiven and Hunter (1976).

The Manor House population contained small size adult snails (six whorls) which displayed a significantly higher average value of T (fig. 12). This suggests the possibility of adoption of progenesis as an adaptive strategy for size decrease in *L. irrorata* (Gould, 1977).

MORPHOLOGICAL VARIATION

The most variable of the measured parameters was translation (T), and this can be



L. IRRORATA ST. CATHERINES ISLAND GA.

Fig. 12. Values of translation rate (T) at each sample station (00 = fossil sample). Error bars are \pm one S.D. Note high T value of Manor House cohort (station 9).

clearly seen in figure 12, by noting especially the contrast between the Manor House (station 9) and English Cut (station 10) localities. Although we can suggest several possible explanations for such morphological variation of T, we have no objective method of assessing the relative merits of the various explanations. As mentioned above, the higher T value at the Manor House locality may be the result of selection for size decrease where "precocious sexual maturation" (Gould, 1977) or acceleration vaulted a juvenile morphology into adulthood. Although progenesis appears to be a likely causal mechanism for such a morphological shift, it does not provide us with an adaptive explanation. In fact, we might, in such a reductionist search for an adaptive explanation, fail to appreciate the possibility that the variation in T reflects passive change in a parameter that is only understood in the context of the organism's Bauplan (Gould and Lewontin, 1979). Possible adaptive explanations for higher T values at

the Manor House locality include (1) selection for small size with increased population density, (2) selection for increased streamlining through decreased cross-sectional area provided by a relatively higher spire and small size (the Manor House locality is subject to higher wave, current, and tidal intensities than the other sample stations) and other possibilities such as (3) increased efficiency of carbonate metabolism with small body size.

Clearly, a decrease in the value of T is correlated with a decrease in the height of the aperture, making the aperture appear rounder. The populations at English Cut and Hokes Landing were closest to the desiccatory environment of a high marsh. These populations had very low S values (fig. 13) and it is possible that variation in T is adaptively related less to body size change than to change in apertural shape.

Measures of whorl expansion (W and W2), as expected, tended to be inversely correlated with T. This agrees with the results of New-

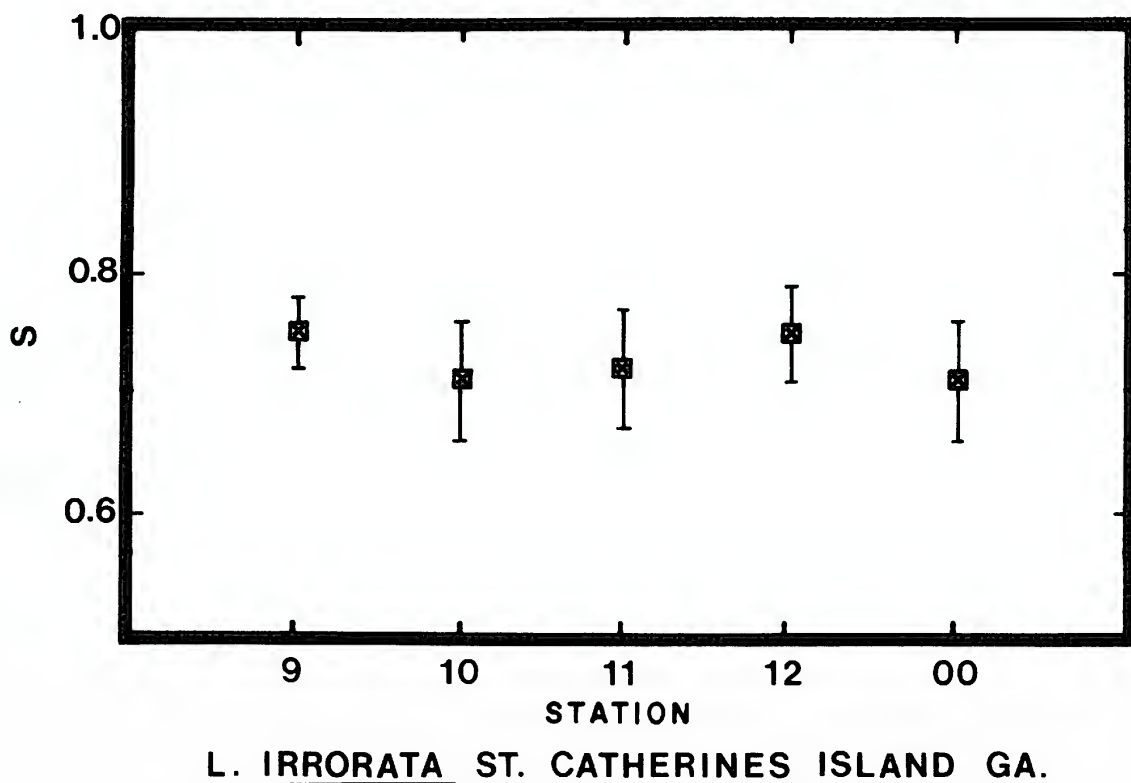


Fig. 13. Variation of apertural shape (S) at each sample station (00 = fossil sample). Error bars are \pm one S.D.

kirk and Doyle (1975). Perhaps the higher whorl expansion rates at the English Cut and Hokes Landing stations are understandable in terms of decreased rigor of the mechanical environment (figs. 14, 15). As usual, alternative explanations exist. Blundon and Vermeij (1983) determined that increased spire height (and, thus, increased suture length) in *L. irrorata* facilitated shell breakage. Possibly, increased rates of whorl expansion (W and W2) at English Cut and Hokes Landing afford greater protection from such predators as raccoons. Our analysis of EF (angle of plane of the aperture) produced homogeneous results (fig. 16). The mechanics of vertical migration of *L. irrorata* up and down *Spartina* stems provide very little variation among stations and we would therefore not expect to see much change in EF, a parameter that has been related to mode of locomotion in gastropods (Linsley, 1977).

FOSSIL POPULATION

The relict muds along Middle Beach have, to our knowledge, never been dated, but similar fossil marsh samples along North Beach have provided uncorrected C-14 dates on shell material that range from 235 to about 3500 B.P. As previously noted, molluscan material from relict marsh deposits on Cabretta flat, Sapelo Island, were radiocarbon dated from 500 to 1000 B.P. (Howard and Frey, 1980; Frey and Basan, 1981).

Only 7 percent of the fossil *L. irrorata* sample exhibited six whorls, the average for adults in living populations on St. Catherines Island. The univariate distribution of shell width (fig. 7D) indicates that mean shell size of the fossil population is comparable with the living cohorts, but smaller individuals are absent from the sample, perhaps the result of postmortem winnowing. The anomaly pre-

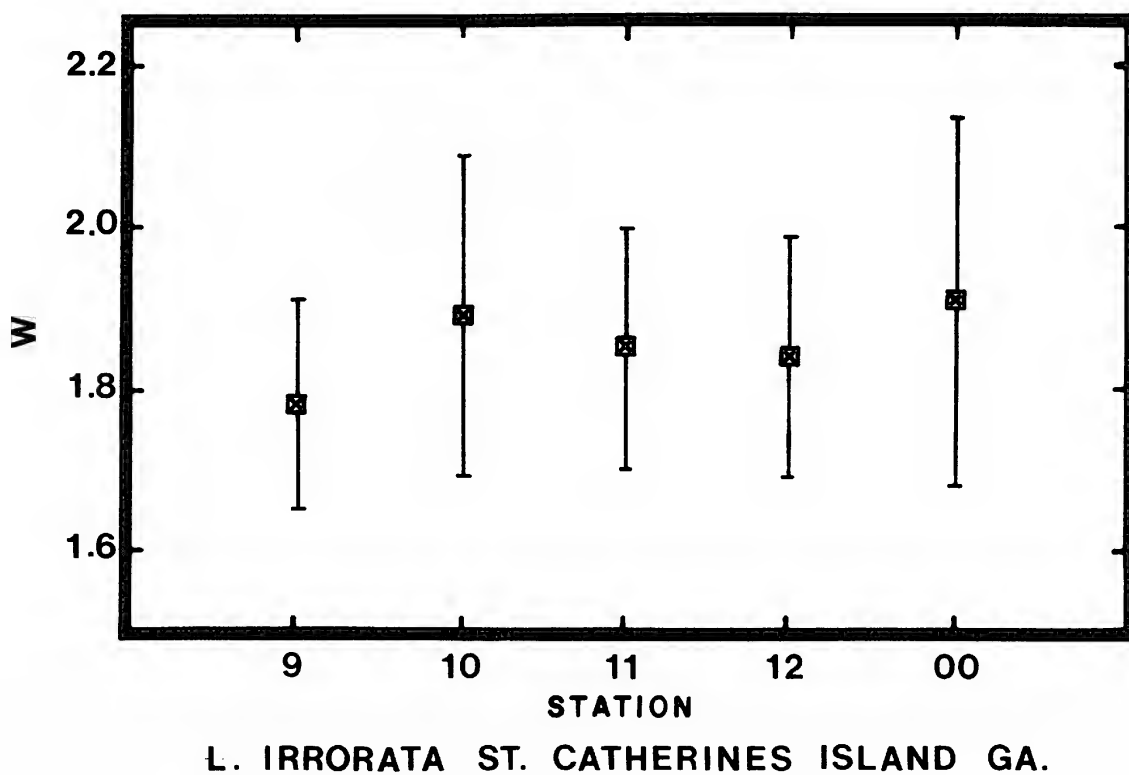


Fig. 14. Variation of whorl expansion rate (W) at each sample station (00 = fossil sample). Error bars are \pm one S.D.

sented by large size individuals with fewer than six whorls is difficult to explain unless one assumes different growth dynamics for the fossil population sample. Conceivably, the fossil sample reflects an environmental setting that is not represented by any of the living cohorts that we examined. The fossil sample has relatively low S values (fig. 13), indicating a protected back-marsh environment.

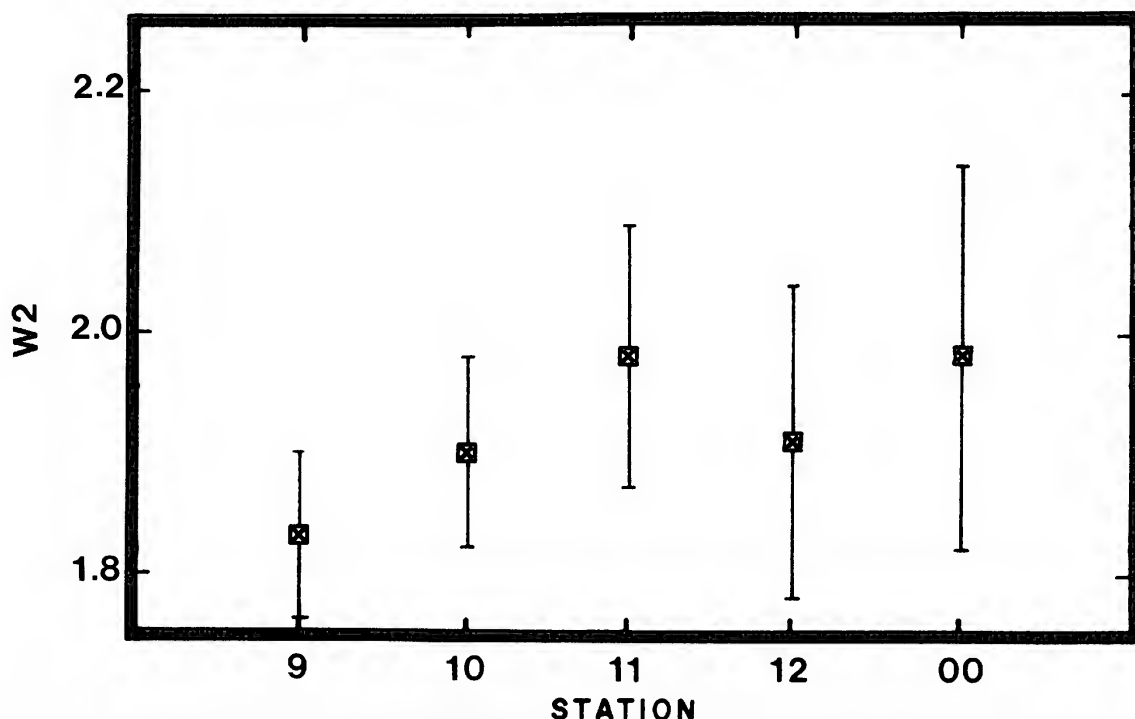
Our analysis indicates that *L. irrorata* is a potentially useful tool for paleoenvironmental reconstructions. The species appears to exhibit limited lateral migration and virtual dependence on *Spartina* grass. This, coupled with the relative isolation of marsh habitats (especially the high marsh) from contiguous coastal habitats, suggests that *L. irrorata* would offer some precision in paleoenvironmental interpretation. On the other hand, Frey and Basan (1981) note that *L. irrorata* possesses no periostracum and is therefore

prone to shell dissolution and that this is intensified in the well-drained sandy high-marsh sediments. Also, as mentioned by Basan and Frey (1977), *L. irrorata* shells can be transported from the high-marsh environment by the tidal migrations of hermit crabs. Nevertheless, *L. irrorata* is probably subject to less taphonomic overprinting than other littorine species which occupy more exposed and more extensive intertidal habitats.

CONCLUSIONS

Our study of the morphology and distribution of *L. irrorata* on St. Catherines Island, Georgia has led to the following conclusions:

1. Standardization of consecutive whorl measurements reveals that living cohorts of *L. irrorata* possess six adult whorls. This may not have been the case for some of the fossil populations of *L. irrorata*.
2. *L. irrorata*, unlike many other littorine



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Fig. 15. Variation of alternative measure of whorl expansion rate (W2) at each sample station (00 = fossil sample). Error bars are \pm one S.D.

species, may prove to be a useful paleoenvironmental indicator. The species has a very restricted habitat and short-term lateral movement is limited. Lateral seasonal migration, not addressed in this study, is probably also limited (Hamilton, 1978).

3. Ecophenotypic variation of *L. irrorata* on St. Catherines Island includes selection of small adult size, possibly via progenesis. The adult size is inversely related to population density. Aperture shape (S) exhibited the least variation and was relatively independent of translation rate (T), whorl expansion rate (W and W2), aperture angle (EF), and total width (TW). Higher apertural areas were correlated with low-marsh environments ("wetter" conditions).

4. Within-habitat variation in *L. irrorata* density predictably correlated with *Spartina* density.

5. Total width of *L. irrorata* proved to be a better indicator of population structure than

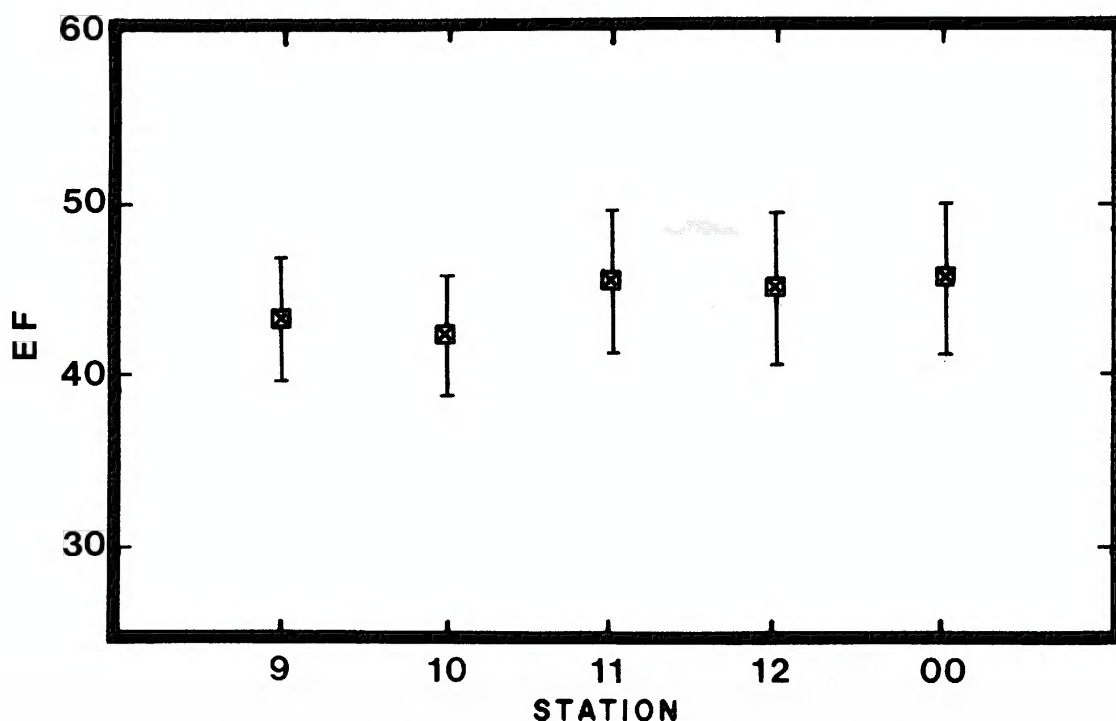
total height and should be used in the construction of survivorship curves of this species.

6. Monitoring cohorts of *L. irrorata* over an 18-day interval demonstrated a relationship between population density and short-term stability of population size.

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Fig. 16. Variation in EF (apertural angle) at each sample station (00 = fossil sample). Error bars are \pm one S.D.

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